Factors impacting sea trout (*Salmo trutta*) populations in changing marine environments

by

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For all of the remarkable women in my life that have taught me, inspired me, pushed me forward and helped me to grow.

Abstract

The brown trout (*Salmo trutta* L. 1758) is a widespread salmonid species that is well known for its multiple life history strategies. Some individuals remain in freshwater for the duration of their lives, and the life stages of these freshwater-resident fish have been well researched. But others implement an anadromous life history strategy where they migrate from their natal river into the marine environment before returning to their natal river to spawn. This life history strategy is beneficial to those individuals by providing them with access to additional food resources in the marine environment which ultimately leads to increased growth rates and fecundity. But with this shift in habitat comes additional risks such as increased predations and exposure to pathogens which can result in an increased level of mortality. Due to the geographic range of these anadromous fish in the marine environment, there are still several large gaps in our understanding of the movements of trout at sea, as well as the associated threats and subsequent impacts they might have on trout populations.

In recent decades, it has been suggested that populations of anadromous trout (or sea trout) are experiencing a decline, however, little research has been done to quantify or explain this observed loss. This same decline was thought to have been observed in Scottish sea trout based on catch numbers, but no national trends have been reported beyond raw catch data reported by the Scottish Government on an annual basis. Using an Information Theoretic modelling approach, three measures of sea trout abundance and a variety of river, geographic and climatic variables were used to explain patterns of change in sea trout populations in Scotland. This study demonstrated overall sea trout numbers have declined 48% in the last 67 years, but that there were significant differences in the trends observed across coastal and regional spatial ranges, with some populations even showing increases in their numbers. Several river specific (river length, river gradient, geology and freshwater loch availability) and climatic variables (mean winter rainfall) were shown to act as consistent driving factors affecting population size change across this time period. One of the most consistently important drivers of sea trout populations was an interaction between river length and geographic region with longer rivers usually producing larger populations. However this relationship varied spatially and temporally and ultimately showed a significant decrease in the resilience of many sea trout populations across Scotland. The strength of the effect of some climatic variables, which vary spatially and

temporally, changed with time and are predicted to continue changing given expected shifts in climate change pressures.

One of the most well documented threats in the marine environment to sea trout populations is the presence of open-net pen Atlantic salmon aquaculture. This industry has been tied to numerous environmentally damaging impacts, including increased parasite levels and increased mortality in wild sea trout populations, in multiple countries in Europe and Scandinavia. The west coast of Scotland hosts one of the largest Atlantic salmon aquaculture industries that has expanded rapidly since the 1970's. There has been little attempt to quantify the impacts of this industry on long term populations trends of sea trout on the west coast. Using an Information Theoretic modelling approach, environmental, climatic and aquaculture focused variables and three measures of abundance were used to identify drivers of change in sea trout populations on the west coast of Scotland over the last two decades. The results demonstrated that sea trout populations are reacting differently in areas with and without Atlantic salmon aquaculture but that these effects are relatively complex. Thus there is a negative effect of production biomass on sea trout populations that can be enhanced or lessened given changes in climatic variables. When sea temperatures rose above 11.0°C, sea trout populations declined with increasing net-pen biomass. During years of low winter rainfall, sea trout populations declined with increasing net-pen biomass. Given the high likelihood that these variables will change in the future due to climate change shifts, it is likely that they will impact sea trout more strongly in future years.

Increased densities of *Lepeophtheirus salmonis*, the salmon louse, are frequently associated with areas of intensive Atlantic salmon aquaculture. At high levels, this ectoparasite can cause extensive physical damage to sea trout that can result in reduced osmoregulatory function and body condition and increased predation and mortality. To examine the range of increased lice densities on wild sea trout, sea trout populations were sampled in five sheltered coastal fjords on the Isle of Skye, Scotland at varying distances from active aquaculture sites (3 km – 48 km). While the likelihood of a sea trout having salmon lice present increased with distance from aquaculture facilities, the total lice burdens were found to be higher on individuals sampled within close proximity (within 13 km) to facility locations. The proportion of different life cycle stages of salmon lice on a sea trout was correlated with the proximity of the fish to aquaculture facilities. For example, the total lice count of a sea trout sampled near an aquaculture facility was

primarily comprised of juvenile lice life stages, while sea trout sampled further away from a facility had a larger proportion of mobile adults and gravid female lice present.

There is still a lack of understanding about the space use by sea trout in the marine environment in Scotland, however, it is suspected that trout populations spend part of their marine life stage in the same sheltered coastal areas that are increasingly occupied by Atlantic salmon aquaculture sites. Given the clear connection to increased salmon lice densities in the water column surrounding the aquaculture facilities in sheltered coastal areas, any overlap between habitat usage by wild sea trout and Atlantic salmon farming could have significant negative impacts on wild fish, particularly vulnerable post-smolts that have entered the marine environment for the first time. Acoustic telemetry techniques were used to gather data on the marine migration and spatial use of two different populations of sea trout post-smolts originating from two adjacent fjord systems located on the Isle of Skye, Scotland. One fjord system contained an active aquaculture facility and one did not. A total of 60 sea trout smolts were tagged and 46 of those individuals were detected on the receiver array. The study demonstrated that sea trout post-smolts maintain a strong fidelity to the coastal fjord system connected to their natal river during the first summer of their marine migration. A small percentage of the detected individuals (13 individuals, 28%) did migrate out of their natal fjord system but most (8 individuals, 17%) returned to that same fjord after a period of time foraging elsewhere. Survival and migration range were not significantly correlated to fish size. A small number of individuals (21% of detected individuals) were detected near the aquaculture facility but there was no significant difference between the amount of time spent near the facility and the amount of time spent elsewhere in the loch.

The four studies presented in this thesis have combined modelling and empirical field study approaches to quantify the historical trends of sea trout populations in Scotland and identify current drivers of those trends. The results presented here can provide future insight to the predicted changes that sea trout populations will experience as their marine habitats undergo continued transformations brought on by both anthropogenic and climatic shifts.

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Author's Declaration

I hereby declare that, except where explicit reference is made to the contribution of others, the material presented in this thesis is the result of original research conducted from November 2015 until April 2020 under the supervision of Professors Colin Adams and Colin Bean and Dr Jennifer Dodd. No part of this thesis has been submitted for another degree.

Isabel Eleanor Moore
April 2020

Chapter 1. General Introduction

Brown trout (*Salmo trutta* Linnaeus 1758) (thereafter trout) is a widely distributed and phenotypically variable salmonid species with native populations found across Eurasia and North Africa (Ferguson *et al*., 2019a; Nevoux *et al*., 2019). Due to their value as a recreational species, brown trout have been introduced by humans to every continent except Antarctica (MacCrimmon & Marshall, 1968; Kershner *et al*., 2019). As a member of the diverse Family Salmonidae, brown trout are closely related to other salmonids such as salmon and charr (Keeley, 2019). Brown trout and Atlantic salmon (*Salmo salar* Linnaeus 1758) are by far the most widespread, well studied salmonids in Europe and Scandinavia.

1.1 Life Cycle and Ecology

The life cycle of the brown trout is one of diverse life history strategies and adaptive migratory patterns, and is thought to be heavily influenced by a variety of environmental and genetic factors (Thorstad *et al*., 2016; Nevoux *et al*., 2019; Fig 1.1). Brown trout reproduce over the autumn months in gravel spawning grounds within a river system although some trout populations are able to spawn in lakes (Northcote, 1997). Their young (i.e. alevins) hatch the following spring and remain in their natal waterbody during an initial juvenile life stage lasting between one and eight years (fry and parr) (Thorstad *et al*., 2016). During this time, fry occupy areas of slow flowing water with a variety of different sheltered habitat such as undercut banks, in-stream vegetation and amongst the substrate of the riverbed (Jonsson & Jonsson, 2011). As the fish grow larger (parr), they are able to move into deep and faster flowing sections of the river, often located further downstream from the spawning habitat. The main prey items for trout during the fry and parr stages are aquatic macroinvertebrates.

However, based on decisions made during the juvenile life stages, the later part of the life cycle of brown trout becomes more complex in terms of individual life history migration strategies (Nevoux *et al*., 2019).

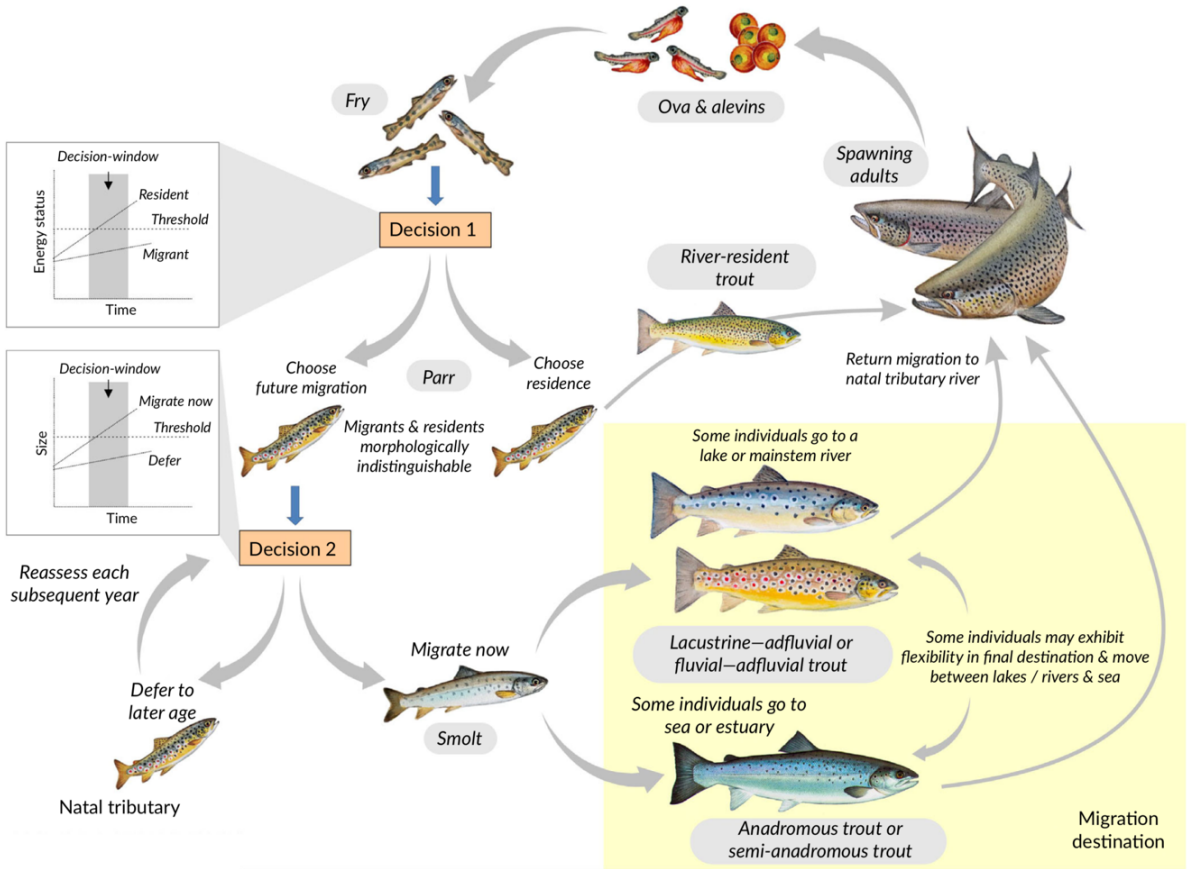


Figure 1.1 The life cycle of *Salmo trutta* (brown trout) with thresholds for migration-residency and age of migration (figure reproduced from Ferguson *et al.*, 2019b).

1.2 Partial Migration and Anadromy

Migration to and from specific habitats in search of advantageous feeding grounds and/or breeding environments is a common adaptation exhibited by a large number of different taxa over a wide temporal and spatial scale (Berdahl *et al*., 2017). For each individual that undertakes a migration, there is a trade of between the benefits associated with new locations and the costs of leaving a known habitat (Jonsson *et al*., 2019). Costs of migration often include increased levels of predation, exposure to new diseases and pathogens, and higher metabolic costs incurred from constant movement (Aldvén & Davidsen, 2017). However, benefits include increased access to nutrient-rich habitats which in turn can increase growth rates, individual physical condition, and ultimately fitness. For anadromous trout (those trout that make migrations to sea), the costs of migration into the marine environment include an inevitable delay to maturation and a decrease in the chance of survival through the increased interaction with predators, pathogens and parasites. The benefits to leaving freshwater include access to better foraging environments and the resultant increase in growth and thus larger body size and ultimately increased reproductive success to those fish that survive (Halttunen *et al*., 2017).

Although migration is considered risky and is often associated with a higher mortality rate than during other periods of the trout life cycle, historically the accompanying increase in growth and fecundity of reproducing adults can increase population size.

Brown trout are well-known for their display of facultative, or partial migration, meaning that a part of the population can remain in their natal river for the duration of their lives, while others can demonstrate a range of migratory patterns to different habitats in both freshwater and the marine environment (Railsback *et al*., 2014; Jonsson *et al*., 2019).

Ferguson *et al*. (2019b) characterised the main life history strategies of brown trout into six categories;

> (1) Lake or river resident- individuals that remain resident in the same section of freshwater catchment where they were born without migrating into another section of the catchment.

(2) Fluvial-adfluvial- individuals will migrate from their natal spawning ground into a larger tributary or the main stem of a river before returning to the same spawning ground as an adult. This strategy can also be referred to as potamodromous.

(3) Lacustrine-adfluvial- individuals that were born in small inlet tributaries migrate into lakes to feed and mature before returning to spawn in their natal tributary. This strategy can also be referred to as potamodromous.

(4) Allacustrine- individuals born in larger outlet tributaries migrate into lakes to feed and mature before returning to spawn as adults in their natal tributary. This strategy can also be referred to as potamodromous.

(5) Semi-anadromous- individuals born in freshwater leave their natal freshwater system and enter into the marine environment, but primarily remain in coastal estuary habitat without moving further into the ocean. Historically, this strategy has been referred to as "anadromous" simply because their movements outside of freshwater systems were not known, but with developments in technology it is now recognized that these fish are not fully entering the open ocean.

(6) Anadromous- individuals born in freshwater migrate from their natal freshwater system into the marine environment and continue into the open sea.

Although these life history strategies have been identified, it is possible to switch between them. For example, there is some evidence of anadromous trout will change their life history strategy to residential after returning to freshwater to reproduce and will remain in the river for the remainder of their lives (Klemetsen *et al*., 2003).

In addition to the terms listed above reported by Ferguson *et al*. (2019b), the following definitions have been outlined below to provide further clarification about the life history strategy terms used in this thesis:

(1) Brown trout/trout: The generic term for the species itself, no life history strategy defined unless specified

(2) Freshwater-resident: An individual trout that resides in freshwater for the duration of its life, although migration through the river system might occur

(3) Anadromy: A strategy wherein a brown trout migrates into salt water for a period of time to feed and gain condition before returning to freshwater to spawn

(4) Anadromous trout: a brown trout that migrates into salt water, estuarine or open ocean, for a period of time to feed and gain condition before returning to freshwater to spawn

The mechanisms that influence the choice of multiple partial migration strategies are still not fully understood (Peiman *et al*., 2017; Archer *et al*., 2020). Historically, it was thought that the size of a fish at a particular time in its life cycle determined whether or not an individual would migrate, however, studies have now demonstrated that this is not an accurate predictor of migratory variation (Acolas *et al*., 2012; Ferguson *et al*., 2019b). Instead, it is clear that both ecological variables (such as available resources and habitats and interspecific competition (Boel *et al*., 2014)) and genetic variance (such as sex, growth rates and ancestral life history strategies (Wysujack *et al*., 2009; Lemopoulos *et al*., 2018)) have some level of influence on a trout's decision to migrate, but ultimately the strength of the effect of factors that facilitate such migration are specific to populations (implying a genetic component to the strategy exhibited) and habitats (implying an environmental component) (Nevoux *et al*., 2019).

Research has demonstrated that during the initial freshwater period of a juvenile trout, an individual will decide to migrate based on its ability to exceed a minimum threshold value of both physiological and genetic conditions at certain life stages (Peiman *et al*., 2017). The genetically determined threshold trait values are thought to vary between populations and individuals, but the general premise of the decision making process is the same. Ferguson *et al*. (2019b) demonstrated that young brown trout must face two threshold trait decisions as juveniles, firstly at an early time period when they become either resident or future migrants, and secondly at a later stage when they choose to either begin their migration the following spring or defer until an even later date. Some research indicates that there could be additional threshold decisions that occur in the later stages of the trout life cycle (del Villar-Guerra *et al*., 2014) and that individuals potentially re-assess their life history strategy decision multiple times over the course of their lives, although this is mostly speculative (Archer *et al*., 2019).

Given that the threshold values appear to vary across populations and individuals, and that if a juvenile defers its decision to migrate for another year, the age at which trout migrate is flexible (Aarestrup *et al*., 2018). Thorstad *et al*. (2016) stated that trout can begin their first migration to sea at any time between one and eight years old.

The outcome of the window of time when a trout must make its migratory decisions depends upon reaching and exceeding a genetically determined threshold. This ability is largely determined by the environmental conditions in which that individual finds itself (Jonsson & Jonsson, 2018). These physiological cues that a fish uses to make this decision are related to various aspects of an individual trout's condition, and are influenced by food and habitat availability and quality, temperature, metabolic and growth rates and hormone levels, all of which are interlinked in determining the physiological condition of an individual. Although the details of the mechanisms that initiate smolting (or do not) are not fully understood, the physiological condition of a young trout, including characteristics such as adiposity (lipid storage) levels, energetic state and metabolic rate, seems to be one of the main drivers determining a migration strategy because it is directly related to whether or not that fish can reach an energy status that is capable of exceeding the minimum threshold trait level (Ferguson *et al*., 2017; Nevoux *et al*., 2019). It is thought that trout that exceed the threshold level are often in top physiological condition, while trout that fall below the threshold are often thought be in poorer condition.

The general rule of thumb in explaining trout migration is that individuals with a high growth rate migrate at a younger age and a smaller size than fish with a low growth rate (Jonsson & Jonsson, 2011). However, it does appear that there is a certain level of plasticity within brown trout cohorts that exceed or fall below the threshold value (Ferguson *et al*., 2019b), indicating that additional physiological factors, tied to extrinsic environmental drivers, could be influencing if and when an individual migrates (Archer *et al*., 2019).

For example, in rivers with restricted food availability, individuals that require more food resources, have a higher metabolic rate and/or have a low growth efficiency will be less able to maintain their condition on the resources within their natal river than those individuals that with lower metabolic rates and/or high growth efficiency (Acolas *et al*., 2012; Rosenfeld *et al*., 2015; Van Leeuwen, 2015). As a result, the individuals with higher metabolic rates but low growth efficiency are potentially more likely to initiate a migratory

life history strategy (either lacustrine or anadromous) in order to find enough resources to sustain themselves.

Lipid content has also been tied to the migratory decisions of brown trout, in that juveniles with a high lipid content are more likely to adopt a resident life history strategy than those individuals with a low lipid content (Jonsson & Jonsson, 2005; Larsson *et al*., 2012; Archer *et al*., 2019). An individual with a high lipid content is able to achieve maturation at an earlier age than an individual with a low lipid content, therefore reducing the need for additional marine resources that would be obtained via an anadromous life history strategy (Sloat & Reeves, 2014). This physiological factor is often tied to water temperature, with lipid content decreasing with increasing temperatures (McMillian *et al*., 2012).

Research has demonstrated that those fish that do not exceed the threshold can display different life history strategies, including remaining in freshwater for additional time in order to build up their condition to a point at which the threshold for migration is exceeded and thus they migrate at a later date (Boel *et al*., 2014). Jonsson (1985) demonstrated that individuals with the fastest growth rates implemented an anadromous life history strategy, while individuals with a medium level growth rate maintained a resident life history strategy and individuals with a slow growth rate did become anadromous, but at an older age than the fast growing cohort. The physiological cues that determine if fish exceed the threshold in any one year or not is a subject of considerable debate (Peiman *et al*., 2017).

Additionally, research has demonstrated that the geographic extent and duration of the marine migration of anadromous trout vary amongst individuals, suggesting that there are further intrinsic and extrinsic drivers influencing migratory decisions beyond the juvenile life stages (del Villar-Guerra *et al*., 2014). These drivers are not yet well understood, but correlations between condition factor and migration distance have been found, with trout in poorer condition migrating further into the marine environment than individuals in better condition (Bordeleau *et al*., 2018).

There is a sex bias between the decision of male and female trout to migrate (Cucherousset *et al*., 2005; Nevoux *et al*., 2019). Female brown trout are more likely in enact an anadromous life history strategy (Klemetsen *et al*., 2003; Thorstad *et al*., 2016). In theory, because of the high energetic cost of reproduction for female trout arising from larger gametes (compared with males), anadromous females are able to achieve higher levels of fecundity and ultimately produce larger ova than freshwater-resident females (Wysujack *et*

al., 2009). Offspring from these large ova seem to have a lower mortality rate than offspring from small ova (Wysujack *et al*., 2009). Meanwhile, while some male brown trout do migrate to sea, there is often a higher proportion of males within a freshwater-resident population than females. Males are less constrained by growth as they are able to achieve effective reproduction capability without the requirement for large body size compared with that of a female (Jonsson & Jonsson, 2018).

In addition to environmental and physiology influences, it has been estimated that 50% of an individual's decision to migrate is driven by genetic differences (Nevoux *et al.*, 2019). Few studies have been able to identify neutral genetic markers that clearly differentiate resident vs. anadromous individuals (Ferguson *et al*., 2019b), but the divergence between life history strategies utilised by trout is thought to be influenced partly by epigenetic modifications, specifically DNA methylation (Baerwald *et al*., 2016). DNA methylation can impact the developmental process resulting in the expression of alternative phenotypes that may not be inherited directly. Research has demonstrated that demethylation is associated with active gene transcription, while increased DNA methylation can result in the silencing of gene expression (Bird 2002). Changes in DNA methylation that can result in gene silencing or transcription are thought to be influenced as early as the embryonic life stage of salmonids by exposure to environmental variables such as temperature (Jonsson and Jonsson, 2019). This connection between methylation and maturation has been observed in Atlantic salmon (Moran & Pérez, 2011) and rainbow trout (Baerwald *et al*., 2016) populations, indicating that the DNA methylation mechanism would be operational across different salmonid species, including *S. trutta*, thus possibly contributing to the facultative migratory decisions of individual brown trout.

A strong link has been shown to exist between the life history strategies of brown trout parents and their offspring, with the majority of young trout implementing the same migration strategy of their parents (Archer *et al*., 2019). However, offspring can exhibit different life history strategies to that of their parents, for example anadromous parents can produce both freshwater-resident and anadromous descendants, as can freshwater-resident parents (Jonsson & Jonsson, 2011). However, anadromous parents produce a higher proportion of anadromous offspring than freshwater-resident offspring. Freshwater-resident and anadromous adults can reproduce together, but the proportion of different descendent life history strategies is not as well understood.

The life history strategy of a trout is in part inherited and thus subject to selection forces. Any major change in the relative costs or benefits resulting from a shift in the environment (such as climate change) may well select against individuals implementing one particular migration tactic but would favour an alternative life history strategy (Nevoux *et al*., 2019). Studies have demonstrated that a shift in migration tactics of a population can occur after only a few generations when trout are exposed to changing environmental conditions (Olsson *et al*., 2006; Sandlund & Jonsson, 2014). For example, if fewer anadromous trout returned to a catchment due to increased mortality in the marine environment, fewer offspring would have a genetic predisposition towards anadromy resulting in a decline in sea trout abundance as well as a larger proportion of the population implementing a resident life history strategy and remaining in freshwater (Gross *et al*., 1988).

However, the decision to migrate is also heavily influenced by environmental drivers (Archer *et al*., 2019). As environmental conditions within freshwater systems continue to change and are expected to worsen through climate change impacts (i.e. water temperatures rising, drought, low oxygenation, spates, etc. (Elliot & Elliot, 2010)), it is possible that the decision making process to go to sea could remain dormant in resident populations until such time as the benefits of leaving freshwater systems outweigh the costs associated with entering the marine environment.

1.3 Smolting and Sea Trout

For a trout parr that choses to migrate into the marine environment, it must first undergo a process known as smolting, at which time it is referred to as a smolt (Thorstad *et al*., 2016). This transition is primarily undertaken in the spring, although timings can differ across rivers in response to environmental factors such as photoperiod, temperature and flow rates (Bohlin, 1993). In some cases, trout parr have been documented moving between freshwater and brackish water without undergoing this process, however, for juveniles to survive in high salinity environments, they must undergo the smoltification process (Flaten *et al*., 2016; Thorstad *et al*., 2016). During this process, the smolt experiences behavioural, physiological and morphological changes which allow it to move from a hypoosmotic freshwater environment to hyperosmotic marine environment (Thorstad *et al*., 2016). Because of the extensive changes that take place during smolting, research has suggested that smolts are under osmotic stress which makes them more vulnerable and potentially at higher risk of predation during this transition from freshwater to salt water (Jonsson & Jonsson, 2009a; Thorstad *et al*., 2016).

Occasionally, anadromous smolts can “de-smolted” (Aarestrup *et al*., 2000; Jonsson & Jonsson, 2011; Thorstad *et al*., 2012). Although the exact causes of de-smolting are unknown, it is thought that water temperature, stress or lack of access to the marine environment due to barriers could encourage a smolt to change its migratory physiology to remain in freshwater (Jonsson & Jonsson, 2011). There is some evidence to suggest that salmonid smolts that undergo a de-smolting process are capable of re-smolting the following year (Shrimpton *et al*., 2000).

Once a smolt has completed the smolting process and has left its natal river for the marine environment, it is identified as a post-smolt until the middle of its first winter at sea (Aldvén & Davidsen, 2017). While at sea, sea trout exhibit a wide range of habitat usage but research suggests that coastal areas and estuaries, particularly around the natal river of sea trout, are critically important to the majority of migrating populations (Middlemas *et al*., 2009; Thorstad *et al*., 2016; Flaten *et al*., 2016). These areas are often nutrient rich and can provide shelter from predators in addition to acting as nurseries for young post-smolts (Aldvén & Davidsen, 2017).

After the post-smolt stage, if an individual is sexually mature, it is commonly referred to as a sea trout and returns to freshwater to spawn (Thorstad *et al*., 2016). In some instances, individuals that are not sexually mature also overwinter in freshwater (Thorstad *et al*., 2016), however they are regionally referred to as finnock in the UK.

Our general understanding of trout life history strategies strongly points to individual fish having a broad range of potential life history options. Within these options even fish that migrate to sea have a continuum of migratory strategies. Within populations, there is evidence that not all individuals act similarly once they enter the marine environment (Thorstad *et al*., 2016). Ferguson *et al*. (2019b) outlined this by categorizing the differences between anadromous and semi anadromous migration strategies but individuals utilizing one or the other would all would be considered sea trout because of their movement through marine habitats.

As such, it is difficult to create a short, yet all-encompassing, definition of the life stage that can accurately define a sea trout. For the purposes of this thesis, the definition of a sea trout follows a similar theme as found in Ferguson (2006), an individual trout that undergoes the smolting process and consequently migrates from its natal freshwater habitat

to the sea to gain condition in the marine environment regardless of its age. Freshwater re-entry, either for spawning or for other purposes, is commonplace amongst sea trout and as long as the individual continues to migrate between freshwater and marine habitat, estuary or open ocean, it would still be considered a sea trout.

1.4 Trout in Scotland

During the last Glacial Maximum (LGM), an estimated 18,000 to 23,000 years ago, much of the UK was covered in ice with little habitat available for fish (McKewon *et al*., 2010). As such, brown trout were restricted to ice-free areas located in northwestern Europe (Ferguson *et al*., 2019a). Because of their likely anadromous heritage, multiple isolated brown trout populations would have been able to expand their range as the ice retreated and colonise available marine areas, including the newly exposed coastlines of the UK and Ireland (McKewon *et al*., 2010; Sanz, 2018). As these previously isolated populations continued their migrations, they overlapped and began interbreeding (McKewon *et al*., 2010). This assimilation between populations, coupled with a range of available habitats and various evolutionarily selection processes such as founder effects and genetic drifts, resulted in the high level of phenotypic diversity observed in Scotland's current brown trout populations (Ferguson *et al*., 2019a).

Brown trout populations are one of three native salmonid species in Scotland (Adams & Maitland, 2018). The other two native salmonids are the arctic charr (*Salvelinus alpinus*) and the Atlantic salmon (*Salmo salar*). There are two other established salmonid populations that have been introduced into Scottish waters, rainbow trout (*Oncorhynchus mykiss*) and brook charr (*Salvelinus fontinalis*).

1.5 Current Status of Brown Trout

Brown trout are listed as a species of Least Concern by the Global ICUN Red List (Wilson & Veneranta, 2019), however, there is little information available about the long term trends in populations of the anadromous brown trout (Lobon-Cervia, 2009; ICES 2016; Wilson & Veneranta, 2019). What is known suggests a complex pattern of population change across Europe and Scandinavia. Hojesjo *et al*. (2017) reported a three-fold increase in sea trout smolt production across Denmark between the 1980's and 2000's and a similar increase in the River Hogsvadson, Sweden between 1980 and 2014. In England and Wales,

returning migrant sea trout increased in the rivers Dee and Fowey between the 1990's and 2010's (Davidson *et al*., 2017) and in catches from six rivers in the north east of England over a similar period (Evans & Harris, 2017).

In contrast, catches (from all methods) in southern Norway rivers showed declines of between 22 and 77% over the period from the 1990's to the 2010's (Hojesjo *et al*., 2017). Similarly 14 rivers in the north west of England showed decreases in catches (Evans & Harris, 2017). Taking all catch records from rivers across England and Wales together, suggests a relatively strong decline in sea trout populations.

In contrast, there is very little known about the national or international status of the freshwater-resident brown trout. There are no national statistics compiled for this life history variant of this species in the public domain.

1.6 Threats to Brown Trout

In a recent ICES report, Wilson & Veneranta (2019) showed that although brown trout are not considered a threatened species, there are still a variety of freshwater environmental variables that can negatively impact juvenile and spawning populations. These variables can be broken into three categories; water quality, water quantity and habitat degradation (Wilson & Veneranta, 2019). Some examples are listed below:

(1) Water quality- the eutrophication of rivers and lakes from point source pollution such as agriculture, the contamination of waterbodies from industrial pollution and pesticides and the acidification of water pH from conifer plantations (Harriman *et al*., 1987) can severely alter water chemistry and damage aquatic populations

(2) Water quantity- human development and management of freshwater systems to control flooding or provide water to cities or agricultural areas often results in loss of water to small rivers that generate important spawning beds and juvenile habitats for brown trout

(3) Habitat degradation- the channelization of rivers by humans and bank erosion stemming from problems such as overgrazing can destroy important freshwater

habitats and also impact a river's natural buffering system to extreme weather events

However, due to the anadromous lifestyle of part of the brown trout population, there are additional threats to sea trout in the marine environment. Research has identified pressures such as fishing exploitation (Limburg & Waldman, 2009), increased levels of predation from predators (Jonsson & Jonsson, 2009a; Aldvén & Davidsen, 2017), a decline in prey such as sandeels (Elliot, 1997; MacDonald *et al*., 2019), and increased exposure to pathogens and diseases as contributing to increased levels of mortality in sea trout (Gjelland *et al*., 2014; Thorstad *et al*., 2015). Additionally, research indicates that climate change and the effects it will have on the natural environment will impact both freshwater-resident and anadromous trout populations (Limburg & Waldman, 2009; Kovach *et al*., 2016; O'Briain *et al*., 2018; Wilson & Veneranta, 2019).

The impacts of climate change are wide ranging and can affect environmental conditions in fresh- and salt water ecosystems. The majority of these impacts that influence trout populations can be broadly divided into temperature, precipitation and flow (Graham & Harrod, 2009; Jonsson & Jonsson, 2011). Research has demonstrated that water temperatures around the world are rising in both rivers and oceans as a result of climate change (Elliot & Elliot, 2010; Nicola *et al*., 2018). Increased water temperatures and the associated lowered oxygen levels have the potential to result in unsuitable conditions for brown trout through their effects on physiology, metabolism and energy demands (Graham & Harrod, 2009), as well as through thermally influenced stress and mortality (Armstrong *et al*., 2003). Changes in migration patterns and habitat use can also be the result of increasing temperatures as individuals seek cooler water such as deeper pools or lakes in freshwater systems or deeper/more offshore locations in the marine environment in order to survive (Fenkes *et al*., 2016; Kristensen *et al*., 2018). Transmittance of fish pathogens and parasites also increase with increasing temperatures, resulting in increased infections and disease risk in already thermally stressed populations in both the marine environment and freshwater (Jonsson & Jonsson, 2011b; Crosbie *et al*., 2020).

In the UK, summers have become drier and winters wetter as a consequence of climate change (Graham & Harrod, 2009). Additionally, the intensity of precipitation falling over short periods of time has increased, often resulting in flash flooding and spates. Navigating river systems in high flows can severely deplete energy reserves, inhibiting migration and spawning success (Fenkes *et al*., 2016). Heavy precipitation during the winter months can

lead to redd washouts, negatively impacting the survival of ova (Jonsson & Jonsson, 2009b). Extremely high or low water flows can also restrict trout movement in river habitats, cutting individuals off from spawning grounds or additional food resources, or result in fish strandings and mortality.

Additionally, the timings of critical migrations, that are driven by water temperatures and flow rates such as smolt runs and spawning periods, would shift as changes in temperatures and flows occurred, resulting in fish moving between fresh- and salt water early or later than they had previously (Jonsson & Jonsson, 2011; Fenkes *et al.*, 2016; Nicola *et al*., 2018). Individuals that migrate at different times would then potentially miss essential feeding opportunities that have historically occurred when they entered the marine environment or miss reproduction opportunities if other fish did not return to freshwater at the same time (Crozier & Hutchings, 2014).

Unfortunately, it is difficult to quantify the effects of each of these threats on sea trout populations and therefore there is a lack of information about what is driving the changes in sea trout populations that have been reported. Problematically, some of these marine threats are likely increasing and potentially worsening (e.g. climate change), indicating that the negative effects they have on sea trout populations could change with time.

1.7 Aquaculture

An example of a growing marine threat that is particularly relevant to Scottish brown trout populations is the impact of aquaculture. The majority of Scotland's aquaculture is dominated by Atlantic salmon that are farmed in open net-pens in shallow, coastal areas along the Scottish west coast and around Scotland's Islands (i.e. the Hebrides, Shetland, and Orkney) (Kenyon & Davies, 2018). The industry has increased exponentially from producing 520 tonnes in 1979 to 189,707 tonnes in 2017 (Munro & Wallace, 2018; Murray & Munro, 2018). Annual Scottish production data reported a 91% increase in the tonnage produced from 1997 (99,197 tonnes) to 2017 (189,707 tonnes) (Fig 1.2). Kenyon & Davis (2018) reported that the industry hoped to increase production to 210,000 tonnes by 2020.

Numerous studies have demonstrated that there is an increased abundance of the naturally occurring ectoparasite, *Lepeophtheirus salmonis* (hereafter referred to as salmon lice) in marine areas of intensive Atlantic salmon aquaculture due to the large number of host species in the open net-pens (Thorstad *et al*., 2015; Moore *et al*., 2018; Thorstad &

Finstad, 2018). Salmon lice attach to a host fish and feed on the mucus and skin of their host (Thorstad *et al*., 2015). In areas where there is no fish farming, natural infection levels range between 0 - 8 lice per fish depending on the time of year, however, as lice infection levels begin to increase so does the amount of physical damage caused to fish (Thorstad *et al*., 2015). Increased levels of salmon lice on salmonids can result in skin and tissue damage, osmoregulatory stress, behavioural changes including early freshwater re-entry which can restrict fish growth rates, increased susceptibility to predation and ultimately increase mortality (Thorstad *et al*., 2015; Halttunen *et al*., 2017).

If densities of salmon lice are not controlled and increase within aquaculture facilities, the larval and mobile stages of the parasite are dispersed from the open net-pens by tidal and wind driven currents into the surrounding coastal areas where they are more likely to come into contact with wild fish that are utilizing the same habitat (Thorstad *et al*., 2015). This overlap in habitat and resulting transfer of pathogens to wild salmonids makes sea trout particularly vulnerable to infection given their suspected preference for coastal areas where aquaculture units are often located (Middlemas *et al*., 2013; Gjelland *et al*., 2014; Thorstad *et al*., 2015).

Research has demonstrated that high levels of salmon lice on sea trout can result in increased mortality and many studies argue that this connection between increasing aquaculture production and lice levels are responsible for some of the declines that have been observed in sea trout populations in recent years (Costello, 2009; Flaten *et al*., 2016; ICES, 2016; Shephard *et al*., 2016; Wilson & Veneranta, 2019).

With the projected growth of Atlantic salmon aquaculture in Scotland, it could be expected that its impact on wild sea trout will become increasingly problematic. However, it is difficult to anticipate the full effects on the populations because very little is known about the marine habitat use of sea trout in Scotland. Luckily, developing technologies are now allowing us insights into fish behaviour in the marine environment that were not possible before. An example of this is acoustic telemetry.

1.8 Telemetry

A variety of telemetry techniques have been used over the decades to track movements in animal populations, including fish. Historically, Passive Integrated Transponder (PIT) and

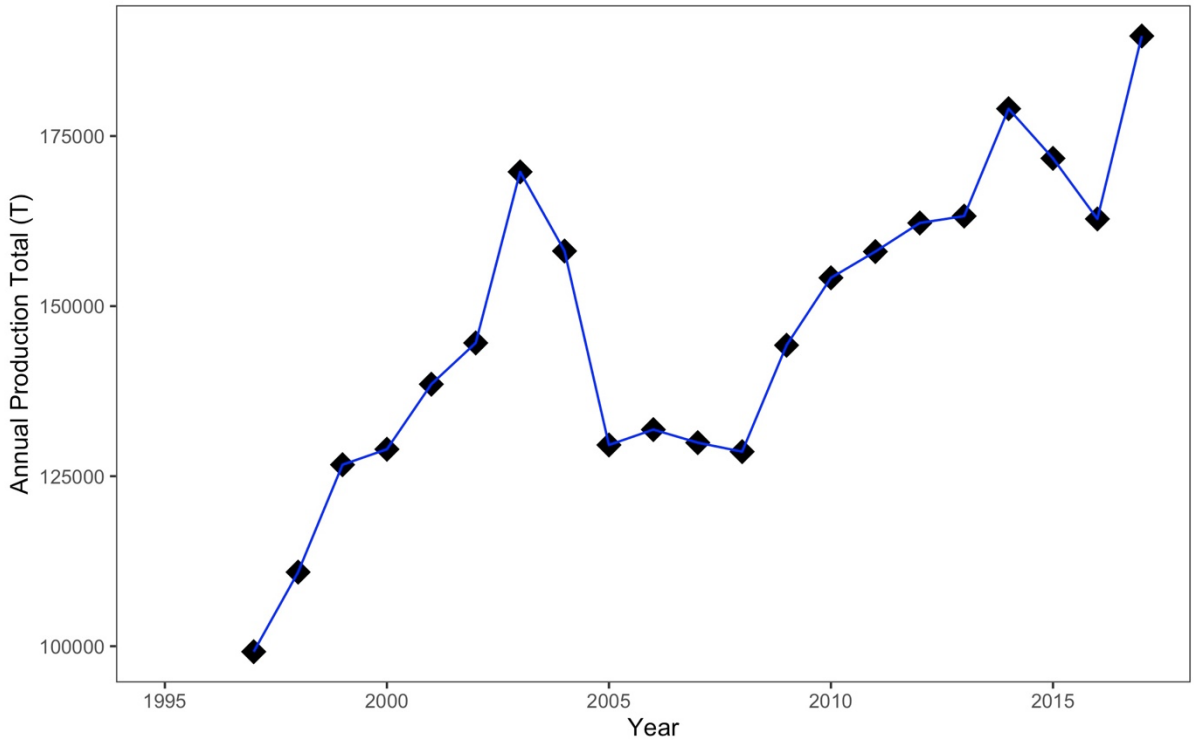


Figure 1.2. Annual production total (T) of Atlantic salmon in the Scottish aquaculture industry (1997-2017). Data from the Scottish Fish Farm Production Survey 2017 (Munro & Wallace, 2018).

radio tags were frequently used in fisheries research and are still used, however, acoustic telemetry is becoming increasingly popular.

Acoustic telemetry is a technique that can be used to track the movements of fish in both marine and freshwaters using the transmission of signals in water. A small transmitter (i.e. a tag) that produces a sound signal at intervals is either implanted into fish or attached externally. Tags can transmit two basic types of signals, continuous and coded. Continuous tags are restricted to one frequency, emitting sequential transmissions with a precise time interval (Skerrit *et al*., 2015). Coded tags transmit a series of "pings" that are unique to an individual tag, which allows multiple tags to use the same frequency. However, if there are too many tags present in the same area, there is a higher possibility of signals becoming mixed, or "tag collision", which results in missed detections. Tag signals are detected by receivers which decodes the tags' transmission. Frequently multiple receivers are deployed as an array to be able to determine patterns of fish movements or habitat use.

Previously, the size of the battery used in acoustic telemetry tags resulted in the overall size of the tag being much larger and restricting their use to studies of larger fish. Advances in battery technology has resulted in a smaller size without compromising the battery life and resulting in reduced overall tag size. This means that the tags can be used in smaller fish, such as salmonid smolts, to answer previously unanswered questions about their movement outside of rivers.

There are still some limitations to acoustic telemetry studies, including the tag effect on individual fish. In order to obtain reliable results from a telemetry study, the tag used should not modify normal behaviour of a fish. Concerns have been raised in the past that negative effects of tagging can include tag expulsions, altered behaviour, reduced swimming efficiency, impaired physical condition and increased mortality (Thorstad *et al*., 2013).

Much research has gone into examining the potential tag effects of a 'V7' tag on salmonids. The V7 is a commonly used tag in salmon and trout smolt studies and was, at the time of the study, the smallest tag capable of transmitting a 69kHz signal that could be detected in the marine environment. Moore *et al*. (1990) and Lacroix *et al*. (2004) both reported from their research that there were no mortalities from tagging with V7 tags. Studies have demonstrated that if V7 tag effects were observed at all, they tended to occur directly after tagging and after a short period of time (a few days to a week), tagged fish

behave similarly to untagged fish (Lucas, 1989; Moore *et al*., 1990; Lacroix *et al*., 2004). Angela *et al*. (2004), Anras *et al.* (2004) and Brown *et al*. (1999) both reported that there was no effect on swimming speed after tagging.

Research has suggested, however, that if any long term tag effects are observed in a study, they are often related to the size of the fish, with smaller individuals experiencing the most negative effects. This is thought to be tied to the impact of tag burden on smaller fish and as such, guidelines have been created to minimise the frequency of negative tag effects. Winter (1983) reported that a tag burden of 2% should not be exceeded in order to minimise effects, however since then, that has been shown to be a conservative estimate. Lacroix *et al.* (2014) recommended that tag burden should not exceed 8% in juvenile salmon and Newton *et al.* (2016) found that there was no short term (~40 days) effect on salmon mortality when fish had tag burdens reaching 12.7%.

1.9 Outline of Thesis

Despite a large body of research on the freshwater stages of the brown trout life cycle, there are still considerable gaps in our knowledge of factors impacting anadromous trout. The general aim of the work presented in this thesis was to add to our understanding of the ecology and status of trout in the marine environment.

Specifically, I address four principal questions (and a number of subsidiary questions) in this thesis:

1) Have the sea trout populations in Scotland changed over time? If so, what are the drivers of that change?

- In Chapter 2, I examine a long term national dataset on sea trout population size from across Scotland and use Theoretically Information modelling to identify drivers of change.

2) Is open net-pen Atlantic salmon aquaculture having an impact on sea trout populations?

- In Chapter 3, I combine a geographically constrained long term dataset of sea trout population size with data from salmon farm production to model the potential for impacts of salmon farming on sea trout populations.

3) Is there evidence that sea lice infection of sea trout in the marine environment is impacted by the presence of open net-pen Atlantic salmon farming?

- In Chapter 4, I examine *L. salmonis* count data collected from five wild sea trout population from coastal areas on the Isle of Skye and use hurdle models to examine the probability of *L. salmonis* infection and the magnitude of that infection in locations of varying proximity to open net-pens as well as the variability in *L. salmonis* life stages on wild sea trout.

4) What coastal zone habitat types are being utilized by sea trout at sea? Is there evidence of an attraction effect on wild sea trout to open net-pen salmon farms?

- In Chapter 5, I use acoustic telemetry techniques in a comparative study of coastal zone use by sea trout in areas with and without open net-pen salmon farms.

Finally, in Chapter 6, I discuss the overall themes of the preceding chapters.

Chapter 2: Drivers of population change in anadromous sea trout (*Salmo trutta*) in Scotland over the last 67 years

Abstract

Reliable assessments of the status of anadromous populations of *Salmo trutta* are few; as a consequence, the IUCN assessment of current population trends as 'unknown'. What data do exist appear to show different patterns in different places. The study presented here used an Information Theoretic modelling approach on a 67 year dataset (1952 to 2018) comprising rod catches from 64 catchments across Scotland to show patterns of change and to identify in river, geographic and climatic drivers of these changes over time.

Over the period of this study, sea trout numbers declined by 48% overall; however, there were strong geographic differences to this pattern. Populations in rivers draining to the East Coast declined, in general, significantly less (13% overall) than those on the West (67%). Of the nine identified Regions in this study, seven showed declines over 67 years, but one Region showed no change and one Region showed an increase in sea trout. Modelling of seven time periods within this time series showed strong spatial effects at regional and catchment levels of sea trout population size as determined by catches and an effect of river length with longer rivers tending towards higher catches. However, there was also an interaction between Region and river length. The strength of the effect of this interaction changed with time and was apparent across Regions as the effect of river length on catch declined towards the end of the time series. This shift suggested that longer rivers with more habitat, and thus potentially more resilient to change, were disproportionately affected in later years. The amount of rainfall in winter had an increasingly complex and overall negative effect on sea trout population size particularly in towards the end of the time series, indicating that rainfall is impacting current Scottish sea trout populations in a way that it was less likely to have done previously. Overall mean river gradient had a positive effect on sea trout numbers, likely because steep river gradients are associated with better quality habitats for trout but possibly also because they provide less good quality habitat for competing salmon. In some Time Periods there was an interaction between river gradient and winter rainfall indicating that the negative effect of high rainfall has a disproportionate effect on rivers with steep gradients, strongly pointing to high rainfall having an effect on sea trout through the action of river spates on overwintering fry and redds. The percentage of peatland and the percentage of calcareous geology within the catchment had counterposing effects on sea trout populations; the former positively

predicting and the latter negatively predicting sea trout population size. Peat catchments are indicative of poor nutrient status, less productive waters which arguably may provide habitat favouring trout populations rather than salmon as a potential competing species. The percentage of standing water in the catchment negatively predicted sea tout population size. This suggests that in rivers with lacustrine habitat, freshwater residency may be favoured over anadromy by trout in these catchments.

A number of the variables predicting sea trout abundance were fixed catchment variables responsible in part for driving the spatial patterns of sea trout population size. However, others were variables that are known to vary temporally, and the evidence of this study is that their strength of effect is changing with time, and under modelled future climate change pressures, are predicted to continue to change.

2.1 Introduction

The brown trout (*Salmo trutta* Linnaeus 1978) is a species native to Europe but now widely introduced across the globe (Sanz, 2018). It is a polytypic species that can adopt a multitude of life history strategies (Klemetsen *et al.*, 2003) which can broadly be divided into non-anadromous (freshwater-resident) and anadromous (sea-run migratory) forms. In many European rivers, the anadromous form of *S. trutta* (hereafter referred to as 'sea trout') (Lobon-Cervia, 2009; ICES 2016) forms the basis of important recreational and commercial fisheries. In many cases these fisheries run alongside those of Atlantic salmon (*S. salar* Linnaeus 1758), and sea trout are often seen as a secondary to them in terms of received interest and research funding (Mills, 1989; ICES 2016).

Reliable assessments of the status of sea trout populations across Europe are few (ICES, 2013; Wilson & Veranta, 2019). This is largely due to the absence of standard data collection procedures across its European range and the lack of agreed biological reference points across a range of habitat types and geographical locations (see ICES, 2013, Höjesjö *et al*., 2017). This lack of standardisation has resulted in a lack of confidence in the actual status of individual populations, and it therefore unsurprising to find that the IUCN Red List assesses the current trend in population or stock status as 'unknown' (Wilson & Veneranta, 2019).

As a result, few studies have examined good quality, long term population data to quantify fluctuations in sea trout populations. Despite this, what data does exist indicate changes in European sea trout populations. In the Baltic Sea, England and the Netherlands, sea trout populations have declined since the 1990's (ICES 2013; Harris & Evans, 2017). In contrast, other countries have seen an increase in numbers. Denmark and Sweden, for example, reported a threefold increase in their sea trout populations between the 1980's and 2010's (ICES, 2013; Höjesjö *et al*., 2017). Geographically contrasting patterns suggest that although there may be a general overall decline in European sea trout numbers, this is not universal and that different populations in different countries across Europe may be subject to different stressors or responding to those stressors in different ways.

The environmental challenges faced by sea trout are many and the magnitude of each of these is likely to vary considerably both between countries and regions. Issues such as habitat fragmentation, losses in habitat quality or quantity due to changes in land or water

use and overexploitation through targeted legal and illegal fisheries and by-catch (often within Atlantic salmon fisheries) are the most commonly cited causes of sea trout decline within Baltic states (ICES, 2013). Losses due to increases in the burden of parasitic sea lice (*Lepeophtheirus salmonis*) are also seen as a key issue in areas where large-scale marine Atlantic salmon aquaculture developments are in place (Thorstad *et al*., 2015; Serra-Llinares *et al*., 2020).

Latitude and water temperature also play a significant role in the survival of cold water adapted species such as sea trout, where the thermal characteristics of rivers, and the availability of prey items can impact the growth, survival and demographic characteristics of salmonids (Jackson *et al*., 2017; Höjesjö *et al*., 2017; Archer *et al*., 2020). Global climate change also brings with it an increased risk of flood, drought, and extreme weather events. These may influence the survival and productivity of sea trout by reducing the suitability of small coastal streams and rivers as nursery areas and for spawning. In coastal marine environments, increased temperatures may bring additional physiological and ecological challenges, the scale of which may also vary between countries.

Other potential effects on Scottish sea trout populations may include overfishing (Hastie & Cosgrove, 2001), acidification from human industrialisation (Moore *et al*. 2017) and extensive conifer plantations (Prodöhl *et al*., 2019) and predation by birds and marine mammals (Harris *et al*., 2008). More controversially, the influences of industrial marine fish farming have been highlighted (ICES, 2013; Shepherd *et al*., 2016). These potential stressors of sea trout populations have been present for decades, however, it is highly plausible that the magnitude of their impact has changed over time.

Although the exact number of sea trout populations is unknown in Scotland, their ability to establish in small coastal channels suggests that they are more widespread and relatively abundant than Atlantic salmon (Milner *et al*., 2006). Whilst the distribution and density of trout may be well understood in rivers where sea trout co-exist with Atlantic salmon, similar data may be relatively rare in rivers where Atlantic salmon are absent. Moreover, difficulties in discriminating juvenile freshwater resident trout from those destined to become anadromous make assessments of recruitment and population size problematic.

This suggests that the most reliable way of assessing the actual status of sea trout is to count the number of emigrating smolts and the number of returning adult fish. In Scotland, limited research has been conducted on long term sea trout population patterns and trends.

Those which are available are restricted in terms of the length of dataset, or to particular catchments or regions (e.g. Pratten & Shearer, 1985; Shelton, 1993; Butler &Walker, 2006; Davidson *et al*., 2017). Pratten & Shearer (1985), for example reported that sea trout captured in commercial netting stations in the North Esk, a large east coast catchment which drains into the North Sea, exhibited a 10-15 year cyclical pattern in abundance. Trends derived from rod and line data have been equivocal, with declines on the north west coast reported by Shelton (1993) and Butler & Walker (2006), but more recent increases in the numbers of rod-caught fish in the River Dee (north east Scotland) (Davidson *et al*., 2017). The possible driving forces behind a decline in sea trout catches on the west coast of Scotland have been examined in a non-peer reviewed book by Jaffa (2018), who concluded that there was no evidence of a negative influence of aquaculture on sea trout population size. This result, however, contradicts a large body of research that demonstrates that the overlap in coastal habitat use by wild sea trout and salmon aquaculture facilities can lead to increased mortality in wild fish driven by dangerously high parasite loads associated with open-net pens (Aldvén & Davidsen, 2017; Moore *et al*., 2018; Thorstad & Finstad, 2018; Serra-Llinares *et al*., 2020).

Despite this study, there has been no systematic national analysis of sea trout population size fluctuations across Scotland and no quantitative analysis of the factors that could be driving population change in Scotland or elsewhere.

Despite a lack of analyses of historical trends in Scottish sea trout populations, there is a large, publicly available, historical dataset of catches of Scottish Atlantic salmon and sea trout from 1952 to the present (Marine Scotland, 2019). The Scottish Government has a statutory requirement for annual returns of all Atlantic salmon and sea trout catches from both commercial and recreational fisheries in Scotland, however, freshwater resident brown trout catches (despite also being *Salmo trutta*) are not required (Marine Scotland, 2015).

This dataset, the “Scottish Salmon and Sea Trout Fishery Statistics (hereafter the SSSTF dataset), comprises the reported numbers of salmon and sea trout captured in 109 “Districts” from three different capture methods, two primarily commercial coastal and estuarine methods (although some records come from freshwater systems) (called “fixed engine” and “net and cobble” fishing), and one recreational (rod and line). In 1994, an additional capture category was introduced to the dataset to separate the number of sea trout that had been captured by rod and line but released from those captured and retained.

In 2004, a separate category for captured finnock (sea trout weighing less than 0.5kg) (Marine Scotland, 2015) was created in addition to adult sea trout catches.

The aims of this study presented here are to use the SSSTF dataset to:

1) determine any long-term temporal changes in sea trout populations in Scotland
2) to define the spatial distribution of any changes
3) to identify potential driving factors influencing sea trout population change

2.2 Materials and Methods

To determine the temporal patterns of sea trout population change and to explore potential drivers of population change over time, here we use geographic, climatic and small and larger scale environmental data as putative predictors of the characteristics of sea trout population size in an Information Theoretic modelling analysis (Grueber *et al*., 2011). An essential precursor to model construction is data cleaning and rationalisation.

2.2.1 Data sources and rationalisation

2.2.1.1 Sea Trout Population Size Data

Sea trout rod and line catches from between 1952 and 2018 (inclusive), were derived from the SSSTF dataset (Marine Scotland, 2019).

Historically, commercial netting was not conducted in all catchments across Scotland and commercial netting for salmonids has declined markedly over the period of this dataset. Thus, commercial net capture data are temporally and geographically skewed; for this reason, we follow the logic of Youngson *et al*. (2002) and used only rod and line catch data in the study presented here. Youngson *et al*. (2002) rationalized that rod catches provided an accurate depiction of salmon abundance trends at an individual catchment level, and used the SSSTF dataset (used in the study reported here) to investigate trends of multi-sea winter (MSW) salmon from 1952 to 1997.

The SSSTF dataset does not provide any measure of fishing effort for the rod fishery (Marine Scotland, 2015). However, rod catch data, uncorrected for effort, has been shown to be a good index of population size. For example, in the UK, several studies have shown

strong linear relationships between rod catch data of Atlantic salmon and data derived from fish counters installed in the same rivers (Beaumont *et al*., 1991; Crozier & Kennedy, 2001). In British Columbia, regional variation in fishery-dependent measures of populations of steelhead trout (*Oncorhynchus mykiss*) abundance has shown similar trends to data from fishery-independent methods (Smith *et al*., 2000). Thorley *et al*. (2005) compared Atlantic salmon rod and line catch data from the SSSTF dataset with counts from fish counters in 12 Scottish rivers and showed similar trends between the two methods.

Thus, we argue that rod catch data generally, and for the SSSTF data specifically, even if not corrected for fishing effort, can be successfully used to analyse the spatial and temporal abundance trends in sea trout in Scotland.

2.2.1.1.1 Data quality control and improvement

Sea trout and finnock (younger and smaller sea trout) are recorded separately in the SSSTF dataset; for the purposes of this study, annual catches of both were combined for further analysis. Additionally, in this study the returns sea trout caught and killed and caught and released also similarly combined.

A total of 106 reporting “Districts”, comprising either single catchments or several neighbouring catchments, reported sea trout rod and line catch data in the SSSTF dataset. To improve data quality and reduce missing data (Grueber *et al*., 2011), 30 Districts that did not have a full catch record history over the 67 years of this study were removed from the dataset. Zero (0) entries to the SSSTF dataset comprised two different types of data: a catch return where no sea trout were captured in that year or where there was no catch return made for that year. Unfortunately, it is not possible to distinguish between these two zero entry types (Marine Scotland, 2015). Districts with records comprising 25% or more zeros across all years were removed from further analysis (11 Districts removed). Thus, a subset of data from 65 Districts were analysed further.

These data were then used to generate three metrics of sea trout population size for each year, for each District separately (Table A1.1).

1. **Sea trout catch**- was determined as the actual reported rod catch of sea trout for that District for each year.

2. **Proportional abundance**- was calculated as the actual annual reported rod catch for that District expressed as a proportion of the total catch from all 65 Districts combined for that year. This metric gave a measure of the relative contribution of that District to the national catch. To meet normality assumptions, proportional abundance was square root transformed.
3. **Rate of population change**- was calculated as the gradient of a single District's rod catch regressed on time (in years) over a defined period. In order to meet model normality assumptions, this metric was then scaled by subtracting the mean of the dataset from each value and then dividing by the standard deviation.

2.2.1.2 Environmental Data

A key element of Information Theoretic modelling is the use of model terms that are likely to be ecologically relevant (Grueber *et al*., 2011). To identify potential drivers of change in sea trout populations, a number of environmental variables with the potential to affect sea trout were identified. The logic for the inclusion of each is presented in Table A1.1. In the first stage of this analysis, ecologically relevant and available environmental data were separated into three categories: River Specific environmental data, Climatic data and Geographic data.

2.2.1.2.1 River Specific environmental data

River specific data were collated for each District from the Scottish Environment Protection Agency (SEPA) "River and loch waterbody nested catchments" dataset (SEPA, 2019). River specific data are available for individual sections of small rivers and lochs (hereafter referred to as "segments") that make up a complete catchment. The data from all of the segments within a catchment were combined together to generate District specific data (calculations for each river specific variable are outlined in Table A1.1). The percentage of lochs within a District was calculated by dividing the SEPA reported total surface area of lochs within a catchment by the total area of the catchment (Table A1.1).

For those Districts comprised of a number of neighbouring catchments (Loch Long, Loch Roag, Little Loch Broom, Kyle of Sutherland and Fincastle Districts) where multiple rivers discharged into a common coastal zone, the data for all of the freshwater catchments flowing into that coastal zone were included in the overall dataset for that District.

One District (Inner District; Isle of Jura) had to be removed because river specific data could not be confidently identified. Thus 64 Districts were analysed further (Table 2.1). Nine river specific environmental variables selected from the SEPA dataset were chosen for their "ecological relevance": river length, maximum river altitude, mean river gradient, the number of combined sewer overflows (CSO) per km in the district, the percentage of the catchment within a 1:10 year predictive flood area, the percentages of calcareous and solid geology within a catchment, percentage of peatland and the percentage of loch surface area in a district (Table A1.1).

2.2.1.2.2 Climatic environmental data

Climatic environmental data were collated from several sources.

The North Atlantic Oscillation index (hereafter referred to as NAO) reports the quantitative changes in sea-level pressure between the Azores and Iceland and is a reputable source of atmospheric variability (Sarafanov, 2009). In the UK, positive NAO values represent mild, stormy weather events, while negative NAO values indicate cold, calm weather. Previous studies have demonstrated that fluctuations in NAO values can be linked to changes in environmental conditions that anadromous sea trout are exposed to in the marine environment, making NAO an important variable to consider in a long-term time series analysis (Honkanen *et al*., 2018). Annual mean NAO data were derived from a historical dataset updated annually by the University of East Anglia (Climate Research Unit, 2019).

Annual mean sea temperature data for four regions around Scotland were taken from the Scottish Ocean Climate Status Report (Hughes *et al*., 2018) (Fig A1.1A). Districts were assigned a sea temperature based on their location in one of those four regions.

Annual rainfall and air temperature data were derived from the UK Meteorological Office data (Met Office, 2019). Region specific data for both rainfall and air temperature were assigned to each district based on their geographic location within the three regions (Fig A1.1B).

Mean seasonal values of rainfall and NAO were separated into mean summer and winter categories. For both of these variables, a summer value was generated by calculating the

Table 2.1. List of the 64 Districts included in this study, divided by Coast and Region.

East Coast	
District Name	Region
Dee	East
Don	East
Forth	East
North Esk	East
South Esk	East
Tay	East
Tweed	East
Ythan	East
Beauly	Moray Firth
Conon	Moray Firth
Deveron	Moray Firth
Findhorn	Moray Firth
Nairn	Moray Firth
Ness	Moray Firth
Spey	Moray Firth
Brora	North
Kyle of Sutherland	North

West Coast	
District Name	Region
Ayr	Clyde Coast
Carradale	Clyde Coast
Clyde	Clyde Coast
Doon	Clyde Coast
Echaig	Clyde Coast
Fyne	Clyde Coast
Girvan	Clyde Coast
Irvine	Clyde Coast
Ruel	Clyde Coast
Stinchar	Clyde Coast
Grudie	North
Hope	North
Kinloch	North
Naver	North
Arnisdale	North West
Broom	North West
Carron	North West
Ewe	North West
Gruinard	North West
Inver	North West
Kanaird	North West
Kirkaig	North West
Laxford	North West
Little Loch Broom	North West
Loch Long	North West
Moidart	North West
Morar	North West
Shiel	North West
Sligachan	North West
Snizort	North West
Creed	Outer Hebrides
Fincastle	Outer Hebrides
Howmore	Outer Hebrides
Loch Roag	Outer Hebrides
Annan	Solway
Cree	Solway
Luce	Solway
Nith	Solway
Urr	Solway
Awe	West
Baa	West
Laggan	West
Leven	West
Lochy	West
Nell	West
Ormsary	West
Pennygowan	West

mean from values reported between April in Year X to September in Year X. A winter value was generated by calculating the mean from values reported between October in Year X to March in Year X+1. The standard deviations of seasonal rainfall were also calculated as a measure of the fluctuations around both summer or winter rainfall means.

Twelve climatic variables were chosen for their "ecological relevance": the linear and second order polynomial of mean sea temperatures, mean air temperatures, mean winter rainfall, mean summer rainfall, mean winter NAO, mean summer NAO, as well as winter rainfall variance and summer rainfall variance (Table A1.1).

All climatic variables were included as second order polynomials because extreme periods of drought or heavy precipitation may have negative impacts by exceeding the optimum ranges for trout (Armstrong *et al*., 2003). For example, the upper lethal limit of temperature for trout is ~25°C and water at this temperature supports only low oxygen levels. Wild salmonids are highly sensitive to such low oxygen levels, in addition to the increasing risk of thermal stress associated with high water temperatures (Graham & Harrod, 2009). The lower lethal limit of temperature for brown trout below 0°C, and while this limit is not often reached, growth rates are limited in colder temperatures (Armstrong *et al*., 2003). Drought and low water flow can result in population isolation and reduced access to habitat (Jonsson & Jonsson, 2009b). High water flows can cause flash flooding, redd washout and fish strandings (Jonsson & Jonsson, 2009b; Fenkes *et al*., 2016). Therefore, it was important to examine the possible non-linear relationships between these climatic variables and the three measures of sea trout abundance.

2.2.1.2.3 Geographic data

Two geographic variables were modelled in this study. The variable Region was defined as a broader geographic area that contained multiple Districts; these are defined in Table 2.1 (additional Regional definitions found in Fig A1.1C). The geographic variable Coast was defined as Districts that fell to the west or east of the central line of Scotland (Fig A1.1D). Both of these variables were included in the modelling.

Many of the variables included in this study were chosen based on their ecological relevance to freshwater life stages of brown trout (Armstrong *et al*., 2003). While these catchment variables do not have a direct impact on sea trout while they are in the marine

environment, they act as driving forces of survival of other life cycle stages, for example the fry and parr that will ultimately become anadromous smolts migrating to sea (Ferguson *et al*., 2019b; Nevoux *et al*., 2019). Ideally, juvenile population data and emigrating smolt numbers for each catchment would be included in this study to provide further information about the carrying capacity and productivity of each catchment, but unfortunately there has been no longer term standardised protocol in place for collecting such data in Scottish rivers.

While there are thought to be many variables impacting sea trout survival at sea, such as food sources, predator levels, commercial fishing and by-catch and other anthropogenic impacts, there is very little localised, long-term, standardised data available, making it difficult to untangle to impacts of threats in the marine environment. Additionally, there is still limited information about how sea trout in Scotland utilise the marine environment, making it difficult to identify which variables would be impacting a population from a single catchment when their habitat usage could extend up to several hundred kilometres from their natal river (Thorstad *et al*., 2016; Kristensen *et al*., 2019b).

2.2.1.3 Variable selection

All of the ecologically relevant environmental variables were selected and tested for collinearity over each time period analysed (see below) (Cade, 2015; Zurr *et al*., 2015). For variables that were highly correlated (>0.7), a single variable that was determined to be the most ecologically relevant, was included for further analysis and remaining correlated variables removed from analysis to avoid replication of variation.

Before modelling began, all selected environmental independent variables were scaled by subtracting the mean of the dataset from each value and then dividing by the standard deviation.

2.2.2 Data Treatment

During initial data exploration, the annual total sea trout abundance for Scotland from 1952 to 2018 was plotted to visually identify any possible trends or outliers (Fig 2.1). To examine potential drivers of change, time periods in the dataset where there was an apparent consistent pattern of population change across the whole of Scotland were defined visually. Eight time periods were thus identified: 1952-1966, 1966-1978, 1978-

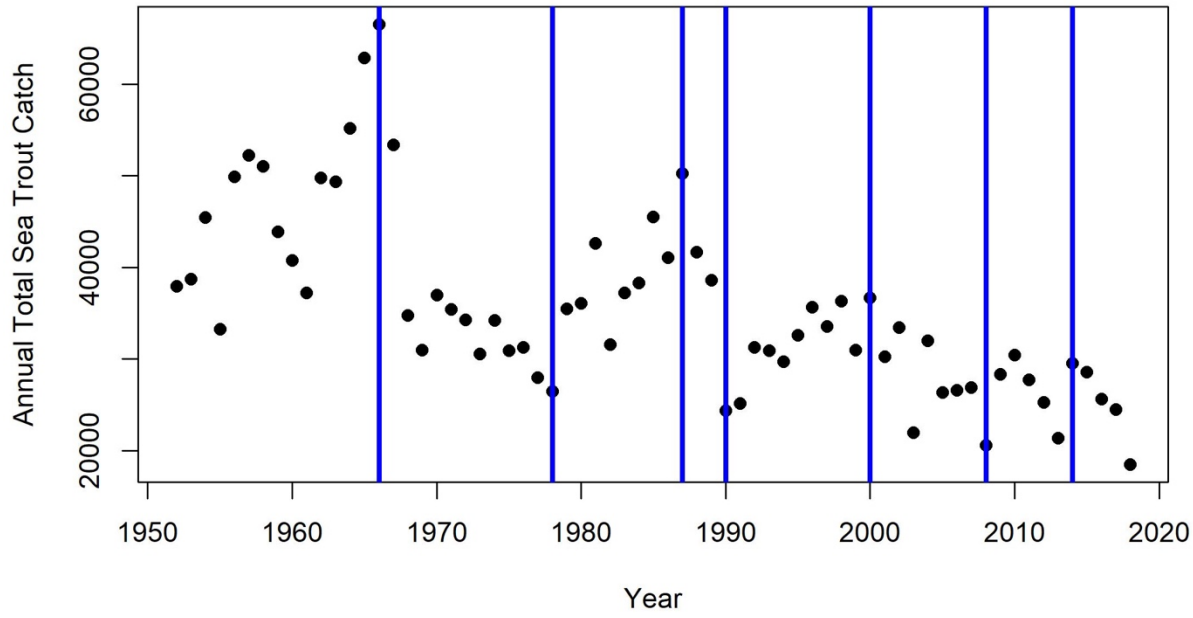


Figure 2.1. Annual total sea trout catch of Scotland between 1952 and 2018. Breaks represent specified Time Periods (defined in Table A1.2) used in the data analysis that were defined visually based on patterns of consistent change in sea trout populations. The final year of a Time Period was also the first year of the following Time Period. For example, 1966 was the last year of Time Period 1966 and the first year of Time Period 1978.

1987, 1987-1990, 1990-2000, 2000-2008, 2008-2014, and 2014-2018 (Fig 2.1). Each of these time periods are hereafter referred to as Time Period X where X is the last year in the subset (Table A1.2). For each of the eight time periods, the relationships between all three measures of abundance and abundance change and environmental variables were modelled separately.

To determine if all Districts were responding similarly to each other during any time period and how this affected the overall rate of change, the standard deviation of the catch rate of each District was used as an independent variable in each rate of change model.

2.2.3 Information Theoretic Modelling

Information Theoretic modelling is a useful modelling method for ecologists because of the robust nature of model selection (Katsanevakis & Maravelias, 2008; Ianellie *et al*., 2016; Walker, 2017). More traditional hypothesis testing is limited by step-wise model selection and the use of AIC units to identify the best model explaining variation, it can often result in several models with very similar AIC values (Grueber *et al*., 2011). In these circumstances, the simplest model of the group is often chosen as the best representative of the relationships in question, however, this method has the potential to eliminate important nuances of independent variables that might be explained by more complex models (Symonds & Moussalli, 2011).

The Information Theoretic approach combines models which cannot be distinguished statistically, by averaging model terms across all models within two AIC units (Grueber *et al*., 2011; Harrison *et al*., 2018). A second advantage of this approach is that model terms are selected through ecological reasoning using the system being investigated (Katsanevakis & Maravelias, 2008). In the study presented here, the variables included in the Information Theoretic modelling approach were thus chosen for their relevance as potentially impacting upon salmonid populations.

2.2.3.1 Overview of modelling process

The development of a final model using the Information Theoretic model was a 5 step hierarchical process (Fig 2.2). These steps were:

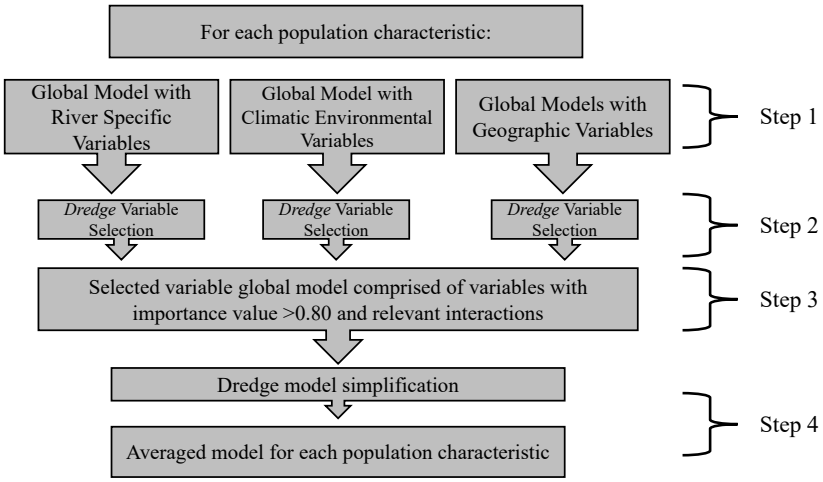


Figure 2.2. Flow chart outlining an overview of the Theoretic Information modelling process.

1. Variable selection: To avoid overfitting the final model, variable selection was undertaken for each of the three categories of explanatory variables (River specific, Climatic and Geographic). For each variable category, each of the three sea trout population metrics (sea trout catch, proportional abundance, and rate of population change) was regressed on the independent group variables separately.
2. Variables from each category were identified for further consideration using the "*dredge*" function in the R package MuMIn (Barton 2019). Variables which appeared in 80% or more of all possible models within 2 AIC units of the model with the lowest AIC value (i.e. a 0.8 model term Importance Value *sensu* (Grueber *et al*., 2011)) were considered further. Model term Importance Values range between 0.00 (i.e. the variable appeared in none of the models that fall within 2 AIC units of the model with the lowest AIC value) and 1.00 (i.e. the variable appeared in all of the models that fall within 2 AIC units of the model with the lowest AIC value).
3. All variables selected at Step 2 (from each of the three categories) were entered in a global model that combined variables from all groups and their interactions.
4. Model averaging was used to produce a final model describing the changes in sea trout population characteristics based on the variable selection process (Steps 1-3). Using the *dredge* function, all models within 2 AIC units of the lowest ranked model were averaged (a full average *sensu* (Grueber *et al*., 2001)) to produce a final averaged model. Model terms that were assigned an Importance Value of >0.80 were defined as highly important, while terms that were assigned an Importance Value of 0.50-0.80 were defined as moderately important (Grueber, *et al.* 2011).
5. Each step was repeated separately for each of the three metrics defining sea trout population characteristics (sea trout catch, proportional abundance and rate of population change).

The initial models (Step 1) included both the fixed effects of all environmental variables and the second order polynomial terms of climatic variables. Using the *dredge* command from the package MuMIn (Barton, 2019), all possible model combinations were investigated to construct a final averaged model (Step 4; Fig A1.2) that combined all the models within two AIC units of the lowest AIC value assigned to a model. If a model term was included in the global model (Step 3) but was not present in the final averaged model (Step 4), it was dropped during model averaging (Grueber *et al*., 2011). This is denoted in future tabular results by the text "Dropped".

The fit of each environmental variable group model was determined by assessing the regression of the modelled dependent variable on the measure of dependent variable. Any outliers identified during these model checks were removed and the model was run again.

A separate Information Theoretic model was developed for each of the three metrics of sea trout population size and rate of change used as response variables. Sea trout catch as a response variable was modelled as a negative binomial distribution, the population rate of change in abundance and sea trout population proportional abundance were modelled as gaussian distributions. Model assumptions were checked by evaluating the regression of modelled and measured values of the dependent variable for all three metrics of populations, as well as by testing for overdispersion.

This methodology was applied for each of the three metrics of sea trout populations (sea trout catch, proportional abundance and rate of population change) for each of the seven identified time periods separately. Time Period 1990 was dropped from further analysis because the subset contained only three years of data and thus would not be able to provide an accurate representation of the factors driving population change in this time period.

2.2.3.2 Reporting potential drivers of population change.

To quantify the relative importance of each variable identified as influencing a sea trout population metric across the whole timeseries, the mean Importance Value for each variable was calculated as the mean of the Importance Values resulting from model dredging of all seven Time Periods (Step 5). Variables with an Importance Value of >0.50 (i.e. of moderately or highly importance) were considered as potential drivers of change.

The strength of a potential driver's influence across the time series was also investigated. The absolute value of the model coefficients of each variable were plotted on all seven Time Periods to visually determine the change in the effect size of each variable's influence on a measure of abundance over time.

All statistical analysis from this study was conducted in R version 3.6.0 (R Core Team, 2019) using packages MuMIn (Barton, 2019), ggplot (Wickham, 2016), MASS (Venables & Ripley, 2002) and plyr (Wickham, 2011).

2.3 Results

2.3.1 General Results

2.3.1.1 Sea trout catch

Reported annual sea trout catches from across Scotland (all Districts combined) varied between years and ranged from 18,467 in 2018 to 66,544 in 1966. The three highest annual catches occurred in 1966, 1965, and 1964 with values of 66,544, 62,865, and 55,152 respectively. The three lowest annual national catches occurred in 2018, 2008 and 2013 with values of 18,467, 20,576 and 21,385 respectively.

There has been a statistically significant decline in sea trout catches in Scotland (all Districts combined) over the 67 years of this study ($P < 0.001$, $b = -0.010$) (Fig 2.3). The model predicted annual sea trout catch in Scotland was 48,593 in 1952 declining to 25,148 in 2018, indicating a 48% decline in sea trout catches during this time period.

Significant differences in sea trout catches between rivers discharging to the East and West coast of Scotland were also apparent ($P < 0.001$) (Fig 2.4). In addition, there was a statistically significant interaction between Coast (East and West) and Year where East Coast rivers showed a considerably lower rate of change in sea trout catches over time compared with the West Coast. West Coast rivers catches were considerably higher at the beginning of the time series in the 1950's than those of the East Coast; by the end of the time series West Coast rivers catches were significantly smaller than East Coast catches. The model predicted values for annual total East Coast sea trout catches was 18,097 in 1952 declining to 15,778 in 2018 (a 13% decline). Model predicted West Coast sea trout catches in contrast, were 30,847 in 1952 and 10,177 in 2018 (a 67% decline).

The three highest reported annual total catches from West Coast rivers occurred in 1966, 1964, and 1965 with values of 37,848, 35,873 and 34,669 respectively, while the lowest annual catches occurred in 2008, 1991, and 1990 with values of 9177, 9207 and 9780 respectively. The three highest annual total catches in the East Coast rivers occurred in 1966, 1965 and 1987 with values of 28,696, 28,196, 25,195 respectively while the lowest annual catches occurred in 2018, 1961 and 1975 with values of 8381, 9523 and 9898 respectively.

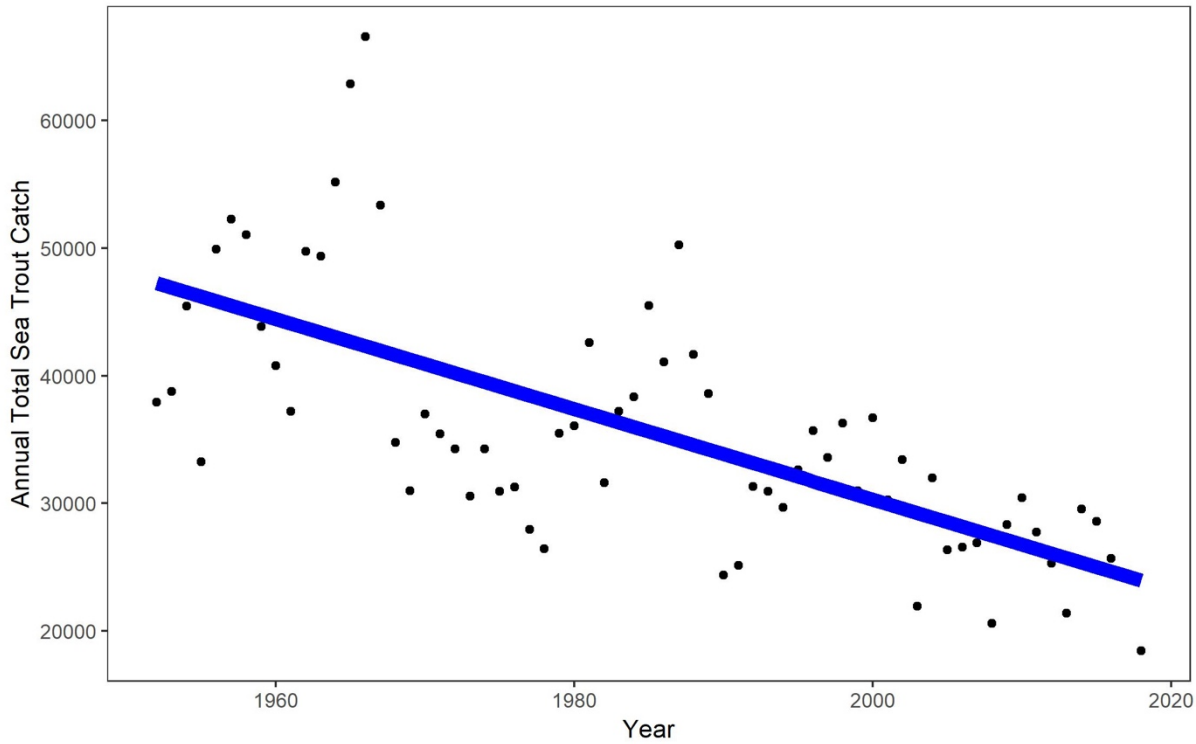


Figure 2.3. Scatter plot of annual total sea trout catch in Scotland (all Districts combined; N=64) with a regression line showing a significant decline with time (1952-2018) (P <0.001).

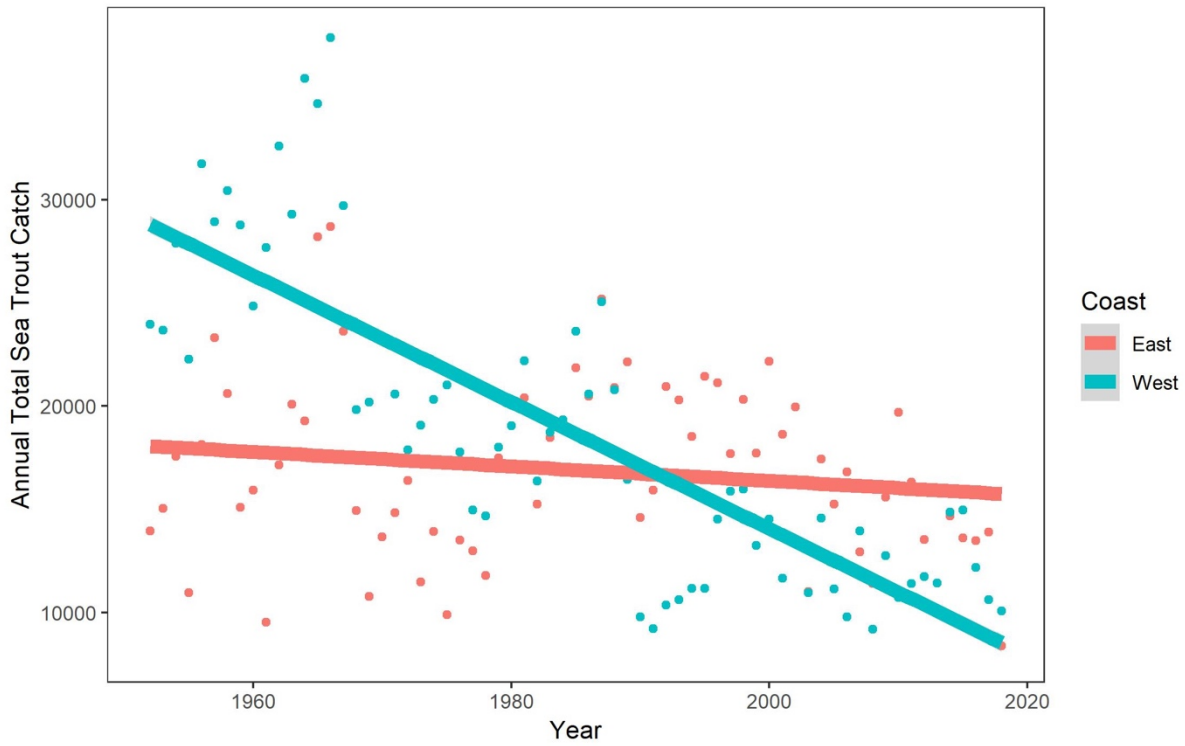


Figure 2.4. Annual total sea trout catches reported from East (N=17) and West (N=47) Coast Districts (1952-2018) regressed on year (P <0.001) with separate regression lines for the predicted values for each Coast.

Out of nine defined geographic Regions (Fig A1.1C), the Moray Firth Region had the highest total sea trout catch across all years between 1952 and 2018 with 467,722, while the West Coast Region had the lowest total catch at 76,123 (Table A1.3). Of the 64 Districts, the Spey District had the highest total sea trout catch over the whole time series at 203,642 followed by the Nith District with 199,965. The Kinloch District had the lowest total sea trout catch at 969, followed by the Little Loch Broom District with 2515 (Table A1.4).

2.3.1.2 Proportional abundance

A total of 2,385,093 sea trout were reported caught in Scotland by rod and line in nine Regions over the whole period of the time series between 1952 and 2018. Of the nine regions, the Moray Firth Region contributed the highest proportional abundance, making up 20% of the total (Table A1.3). The Region that contributed the least was the West Coast that only produced 3% of the total (Table A1.3).

Of the 64 Districts, the Spey, Nith and Ythan Districts had the highest proportional abundance, producing 9%, 8% and 7% of the total reported catch overall years respectively (Table A1.4). The Kinloch, Little Loch Broom, and Pennygowan Districts had the lowest proportional abundance over the time series, producing <0.001%, 0.001% and 0.001% respectively (Table A1.4).

2.3.1.3 Rate of change

Of the nine Regions across Scotland (Fig A1.1C), seven showed an overall negative rate of change in reported catch of sea trout between 1952 and 2018. The Clyde Coast Region demonstrated the greatest decline, indicating that sea trout abundance declined the fastest in this area ($P < 0.001$, $b = 0.026$) (Table A1.3). The Outer Hebrides demonstrated the lowest rate of change ($P = 0.733$, $b = -0.001$) (Table A1.3). The East ($P < 0.001$, $b = 0.016$) and North ($P = 0.211$, $b = 0.004$) Regions showed a positive rate of change indicating that over time, reported sea trout catch rate increased in this area (although in the case of the North Region, this change was not significant).

At a District level, the majority of the 64 Districts (N=42) exhibited a negative rate of change in reported sea trout catch over time (Table A1.4). Of these 42, 36 were districts on

the West coast and six were on the East coast. The remaining 22 Districts showed a positive rate of change, 11 from the West coast and 11 from the East Coast.

The three Districts with the most negative rate of change in reported sea trout catches, were Morar ($P < 0.001$, $b = -0.085$), Carradale ($P < 0.001$, $b = 0.062$), and Awe ($P < 0.001$, $b = -0.058$). The Districts with the most positive rate of change in reported catches, were Naver ($P < 0.001$, $b = 0.048$), Kinloch ($P < 0.001$, $b = 0.044$), and Tweed ($P < 0.001$, $b = 0.034$). The three Districts that showed the least change in sea trout catch were Hope ($P = 0.921$, $b < 0.001$), Tay ($P = 0.852$, $b < 0.001$) and Carron ($P < 0.878$, $b < 0.001$).

2.3.2 Modelling Drivers of Sea Trout Population Change

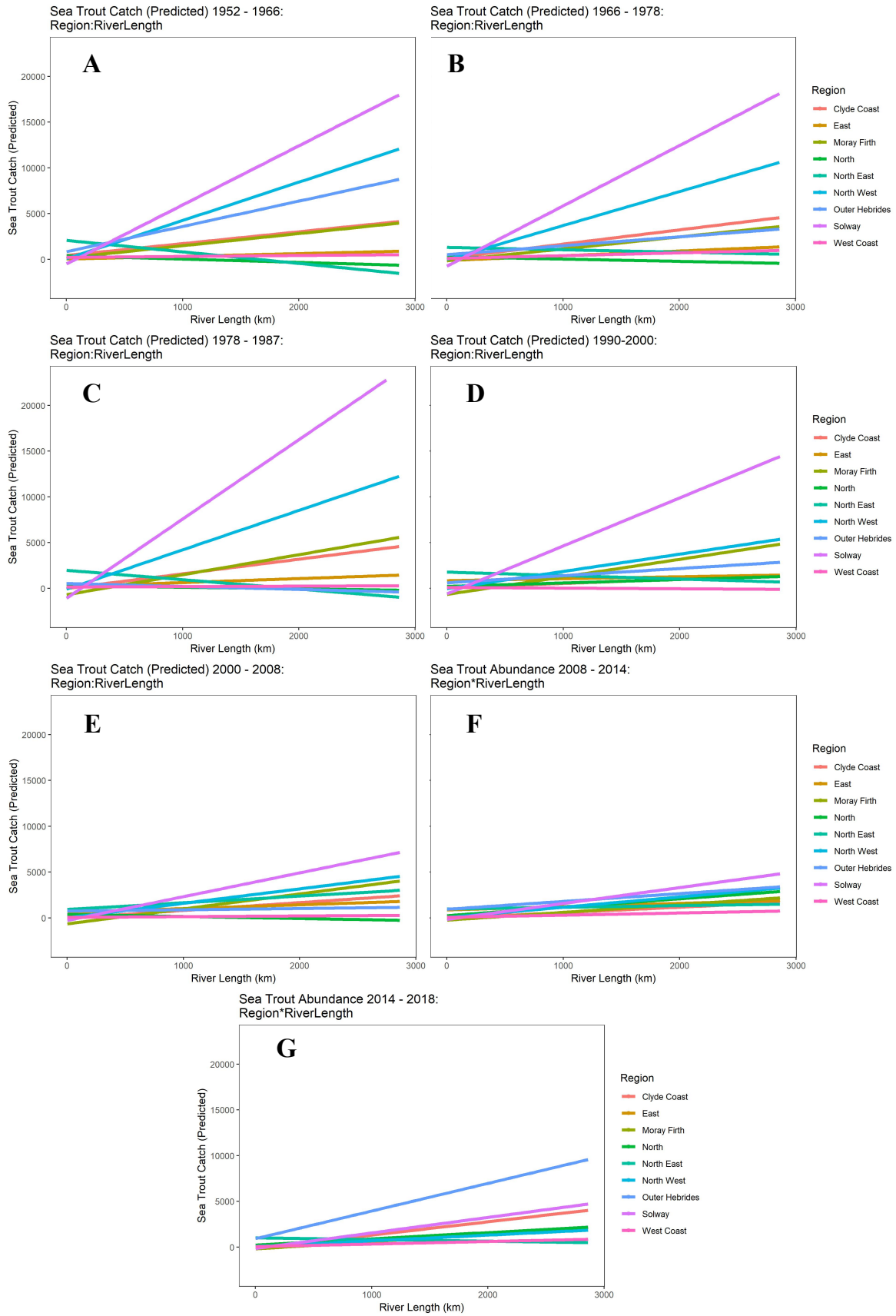
2.3.2.1 Sea trout catch

Six catchment and climatic variables and their interactions were identified by the Information Theoretic modelling as important in predicting sea trout catches across the modelling of the seven time periods of the dataset examined here.

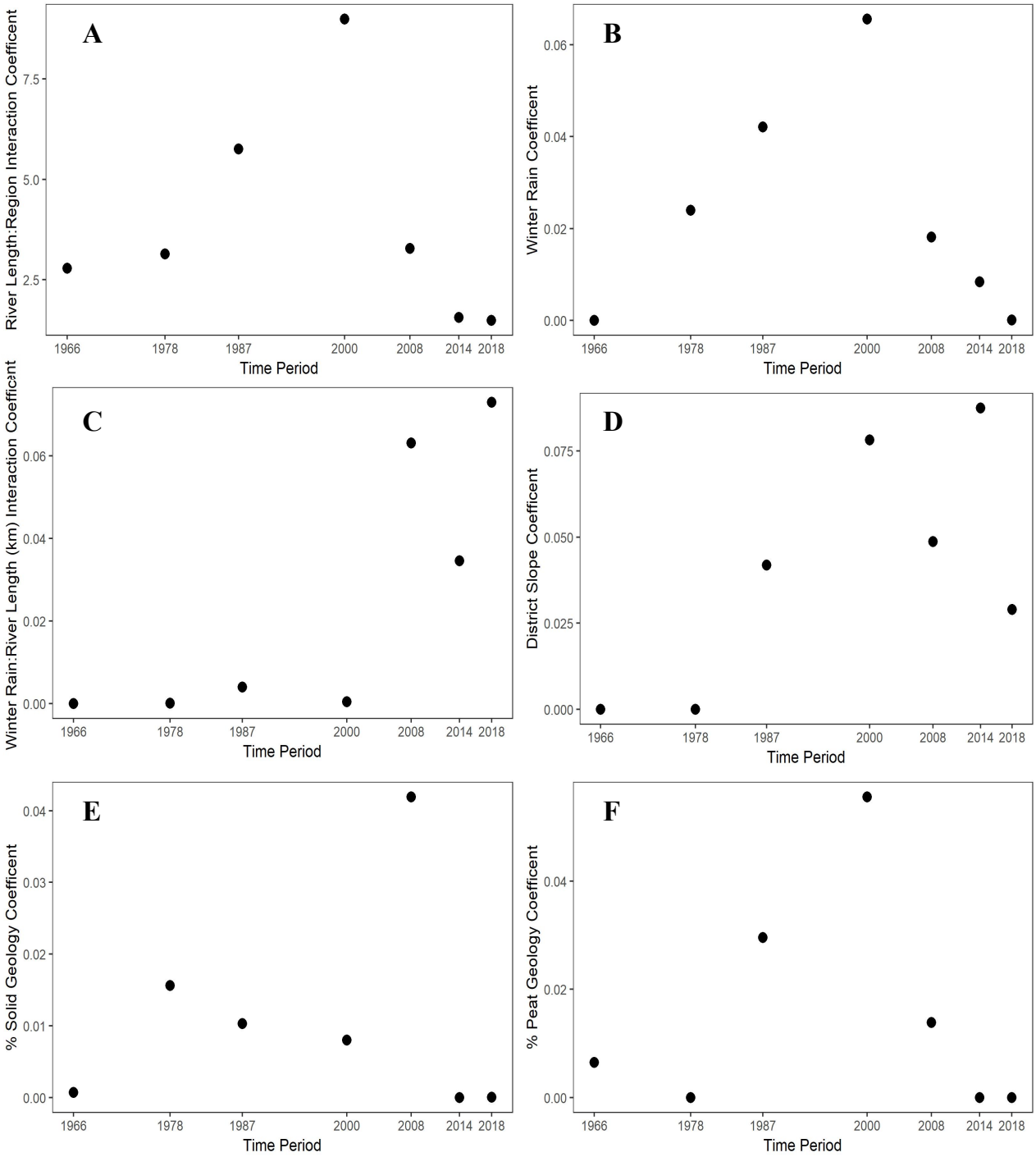
Region and river length

In general, sea trout catch increased with increasing river length but there was a consistent important interaction between river length and Region across all Time Periods (Figs 2.5A-G). The strength of the interaction's effect however, changed over Time Periods (Fig 2.6A). Early Time Periods showed differences between Regions in the effect that river length had on the number of sea trout caught (Figs 2.5A-B; Fig 2.6A). By the middle periods of the time series, differences between Regions became more pronounced (Figs 2.5C-D; Fig 2.6A). By the later part of the dataset, the interaction strength and thus the variability between Regions had reduced (Figs 2.5E-G; Fig 2.6A). These data strongly suggest that the strength of the interaction initially increases in effect and then markedly declines such that the regional variation is much smaller by the end of the time series compared with earlier periods. More regional detail for each Time Period is available in Appendix 1 (A1.1-A1.7). The mean of the Importance Values assigned to this interaction term by the model dredging process across all seven Time Periods was 1.00, indicating that this interaction was highly important and was included in all of the models within two AIC units of the model with the lowest AIC in every Time Period.

Winter rainfall



Figures 2.5A-G. River length (km) and geographic Region on predicted sea trout catch numbers showed a significant interaction across specified Time Periods. A- Time Period 1966; B- Time Period 1978; C- Time Period 1987; D- Time Period 2000; E- Time Period 2008; F- Time Period 2014; G- Time Period 2018.



Figures 2.6A-F. The effect size of important variables (Importance Value >0.50) and their interactions predicting sea trout catch trends across all seven Time Periods. Plotted to show the pattern of influence of each variable on sea trout catch over time. A- Absolute values of mean model coefficients of the interaction between river length and geographic Region. B-Absolute values of model coefficients of winter rainfall. C-Absolute values of model coefficients of the interaction between region and winter rainfall. D- Absolute values of model coefficients of District mean river slope. E- Absolute values of model coefficients of the percentage of solid geology in a District's catchment area. F- Absolute values of model coefficients of the percentage of peat geology in a District's catchment area.

Mean winter rainfall (mm) was an important negative predictor of sea trout catch in six of the seven Time Periods modelled (1978, 1987, 2000). Thus, in these periods, higher rainfall was associated with lower sea trout catches. The strength of the effect of winter rainfall changed over the dataset firstly increasing then decreasing (Fig 2.6B). Although there was no effect in Time Period 1966, over time the effect of winter rainfall on catch strengthened until Time Period 2000, after which it declined again. The mean Importance Value assigned to this model term by the model dredging process across the seven Time Periods was 0.86 indicating that it was a highly important variable.

Winter rainfall and river length interaction

Modelling identified an important negative interaction between river length and winter rainfall on sea trout catch in three of the seven Time Periods modelled (2008, 2014, and 2018). These data suggested that higher numbers of sea trout were caught in longer rivers than in short rivers when winter rainfall was below 100 mm. As winter rainfall increased, sea trout catches declined in all Districts regardless of river length, however, longer rivers continued to report higher sea trout catches than shorter rivers. Thus, the positive effect of river length on sea trout catches was reduced by the effect of increased winter rainfall. The effect of the interaction strengthened continuously over time from earlier to later Time Periods (Fig 2.6C). More detail on these interactions for each Time Period is presented in Appendix 1 (A1.5-A1.7). The mean Importance Values assigned to this model term by model dredging across the seven Time Periods was 0.55, indicating that this interaction was moderately important.

Mean river gradient

The mean river gradient of a District was an important positive predictor of sea trout catch in five of the seven Time Periods modelled. Thus, geographic areas with greater river gradient had higher predicted sea trout catches. The effect of this variable generally increased with time over the dataset (Fig 2.6D). Early Time Periods showed no effect of river gradient, the effects strengthened in the middle period of the time series, before weakening slightly again in the final modelled Time Period (2018). In Time Period 2008 (only), there was an important interaction between gradient and summer rainfall in its effect on sea trout catch. The positive effect of river gradient on sea trout catches was reduced by the influence of summer rainfall in this Time Period. In Time Period 2014 (only), there was a significant interaction between river gradient and the polynomial of winter rainfall. The positive effect of river gradient on sea trout catches was thus reduced by the influence of winter rainfall in this Time Period. More detail can be found about

these relationships in each Time Period in Appendix 1 (A1.3-A1.7). The mean of the Importance Values assigned to this model term by model dredging across the seven Time Periods was 0.71, indicating that this variable was moderately important.

Percentage of solid geology

The percentage (%) of solid geology in a District's catchment area was an important negative predictor of sea trout catch in four of the seven Time Periods modelled. Districts with a higher percentage of the catchment surface area comprising solid (and consequently a lower percentage of drift geology in the catchment) had a lower sea trout catch. The strength of the effect of the solid geology percentage was not consistent across time periods in the dataset (Fig 2.6E). Early Time Periods showed a relatively weaker effect of the percentage of solid geology on catch, it strengthened markedly in the 2008 Time Period and subsequently decreased in later Time Periods. More detail can be found about these relationships in each Time Period in Appendix 1 (A1.2-A1.5). The mean of the Importance Values assigned to this model term by model dredging across the seven Time Periods was 0.67, indicating that this variable was moderately important.

Peatland dominance

Peatland dominance within a District's catchment area was an important positive predictor of sea trout catch in four of the seven Time Periods modelled. Thus, Districts with a higher peatland dominance in the catchment had a higher predicted sea trout catch. The strength of the effect size of peatland dominance was not consistent across Time Periods, having a relatively stronger effect in the middle period of the dataset, before it declined in influence in the 2014 and 2018 Time Periods (Fig 2.6F). More detail can be found about these relationships in each Time Period in Appendix 1 (A1.1, A1.3-A1.5). The mean of the Importance Values assigned to this model term by the model dredging process across the seven Time Periods was 0.57, indicating that this variable was moderately important.

2.3.2.2 Proportional abundance of sea trout

Seven catchment and climatic variables and their interactions were identified by the Information Theoretic modelling as important in predicting the proportional abundance of sea trout across models derived for the seven time periods of the dataset examined here.

Region and river length interaction

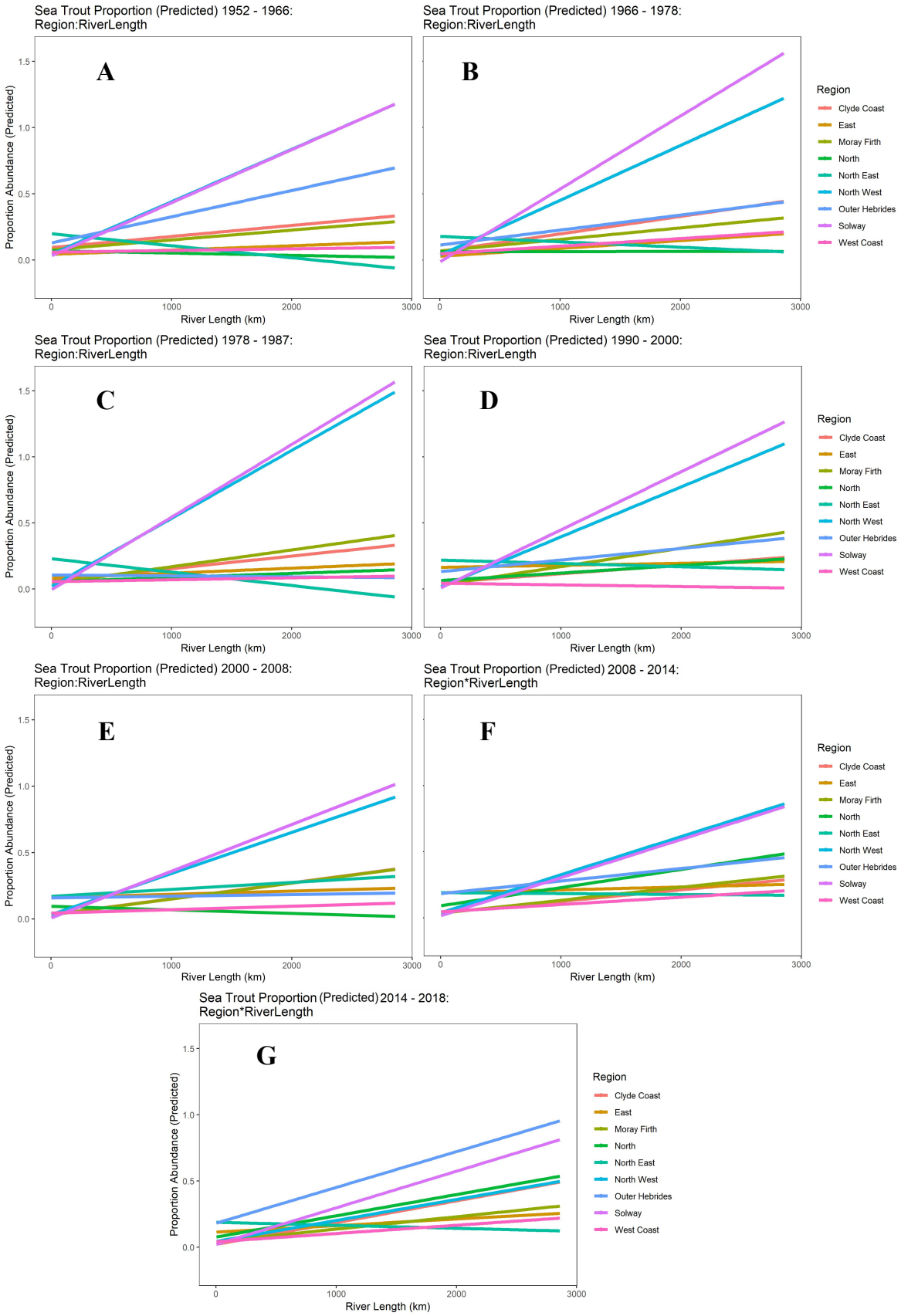
As with simple sea trout catch, there was a general positive effect of river length on the reported proportional abundance of sea trout, thus longer rivers were generally associated with higher proportional abundance, but there was a consistent important interaction between river length and Region across all Time Periods (Figs 2.7A-G). The strength of the effect of the interaction changed over time across the dataset (Fig 2.8A). Early Time Periods showed clear differences between Regions in the magnitude of the effect of river length on proportional abundance of sea trout (Figs 2.7A-B; Fig 2.8A). By the middle period of the dataset, differences between Regions became more pronounced (Figs 2.7C-E; Fig 2.8A). By the later part of the dataset, interaction strength and variability had reduced (Figs 2.7F-G; Fig 2.8A). These data strongly suggest that the strength of the interaction initially increases in effect and then markedly declines, such that the regional variation was much smaller by the end of the time series compared with earlier periods. More regional detail in each Time Period is available in Appendix 1 (A1.1-A1.7). The mean of the Importance Values assigned to this interaction term by the model dredging process across all seven Time Periods was 1.00, indicating that this interaction was highly important and was included in all of the models within two AIC units of the model with the lowest AIC in every Time Period.

Winter rainfall and river length

There was an important negative interaction between river length and mean winter rainfall in predicting the proportional abundance of sea trout in five of the seven Time Periods modelled. Generally, longer rivers predicted a decreasing proportional abundance of sea trout as winter rainfall increased. Shorter rivers predicted a smaller proportional abundance than longer rivers, but demonstrated a similar decline in proportional abundance as winter rainfall increased. Thus, the positive effect of river length on proportional abundance was reduced by the effect of winter rainfall. The strength of the effect of this interaction changed with time over the dataset (Fig 2.8B); generally strengthening through the dataset, except in Time Period 2014 when the effect noticeably weakened before strengthening again in Time Period 2018. More detail can be found about these interactions for each Time Period in Appendix 1 (A1.3-A1.7). The mean Importance Value assigned to this model term by model dredging across the seven Time Periods was 0.79, indicating that this interaction was highly important.

Percentage of calcareous geology

The percentage of calcareous geology within a District's catchment area was an important negative predictor of the proportional abundance of sea trout in four of the seven Time



Figures 2.7A-G. The effects of a significant relationship between river length (km) on predicted proportional abundance of sea trout and its interaction with geographic Region across specified Time Periods. A- Time Period 1966; B- Time Period 1978; C- Time Period 1987; D- Time Period 2000; E- Time Period 2008; F- Time Period 2014; G- Time Period 2018.

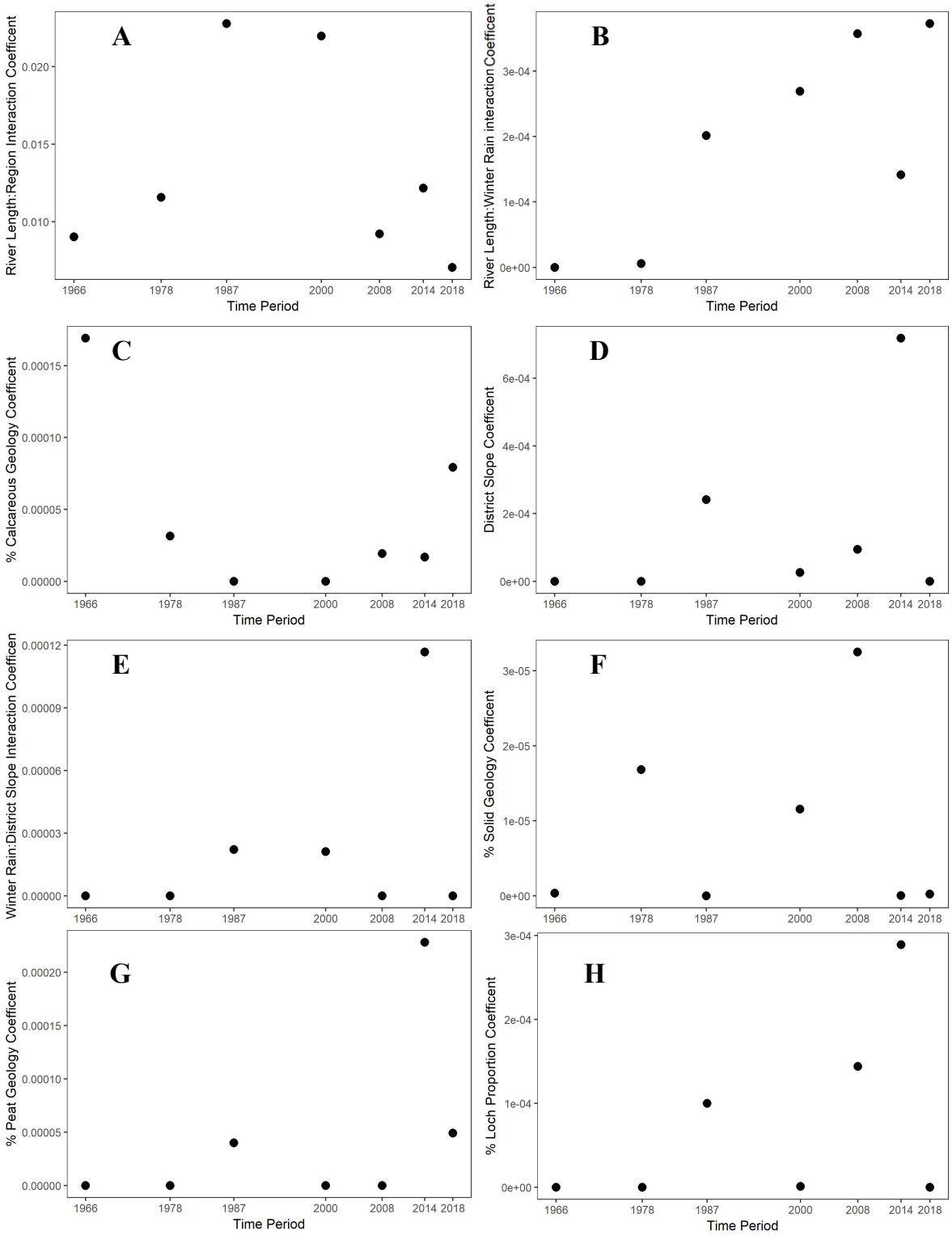


Figure 2.8A-H. The effect of important variables (Importance Value >0.50) and their interactions predicting sea trout catch trends across all seven Time Periods. Plotted to show the pattern of influence of each variable on sea trout catch over time. A- Absolute values of mean model coefficients of the interaction between river length and geographic Region. B- Absolute values of model coefficients of the interaction between river length and winter rainfall. C- Absolute values of model coefficients of the percentage of calcareous geology in a District's catchment area. D- Absolute values of model coefficients of District mean river slope. E- Absolute values of model coefficients of the interaction between District mean river slope and winter rainfall. F- Absolute values of model coefficients of the percentage of solid geology in a District's catchment area. G- Absolute values of model coefficients of the percentage of peat geology in a District's catchment area. H- Absolute values of model coefficients of the percentage of peat geology in a District's catchment area.

Periods modelled. The greater the percentage of calcareous geology, the lower the predicted proportional abundance of sea trout. The strength of the effect of calcareous geology generally weakened then slightly strengthened across the dataset (Fig 2.8C). In the 1966 Time Period, there was a strong effect of calcareous geology on proportional abundance, but this effect weakened noticeably in the middle period of the dataset. The effect began to increase its strength again in the later Time Periods but did not reach the same level of influence as previously. More detail can be found about this relationship for each Time Period in Appendix 1 (A1.1, A1.2, A1.5-A1.7). The mean of the Importance Values assigned to this model term by the model dredging process across the seven Time Periods was 0.70, indicating that this variable was moderately important.

Percentage of solid geology

The percentage (%) of solid geology within a District's catchment area was an important negative predictor of the proportional abundance of sea trout in three of the seven Time Periods modelled. Thus, catchments with a high percentage of solid geology had a generally lower proportional abundance of sea trout. Although the strength of the effect of the percentage of solid geology varied over time, there was no obvious pattern of change across the time series (Fig 2.8F). The small effect of the percentage of solid geology generally remained the same through the dataset, except in Time Period 2008 when the effect noticeably strengthened before weakening again by Time Period 2018. More detail can be found about this relationship for each Time Period in Appendix 1 (A1.2, A1.4, A1.5). The mean of the Importance Values assigned to this model term by the model dredging process across the seven Time Periods was 0.56, indicating that this variable was moderately important.

Mean river gradient

The mean river gradient of a District was an important positive predictor of the proportional abundance of sea trout in four of the seven Time Periods modelled. Thus, catchments with greater river gradient showed higher proportional abundance rates. Although the size of the effect of this variable changed over time, there was no obvious patterns of change (Fig 2.8D). The small effect of mean river gradient generally remained approximately the same through the dataset, except Time Period 2014 when the effect noticeably strengthened before having no effect on the Time Period 2018 model. More detail can be found about this relationship for each Time Period in Appendix 1 (A1.3-A1.6). The mean of the Importance Values assigned to this model term by model dredging

across the seven Time Periods was 0.56, indicating that this variable was moderately important.

Additionally, an important negative interaction between mean river gradient and the polynomial of mean winter rainfall occurred in three of the seven Time Periods modelled. Generally, a significantly higher proportional abundance was reported in Districts with a lower mean river gradient than in Districts with a higher river gradient when winter rainfall levels were high. However, in Time Period 2014, a significantly higher proportional abundance was reported in Districts with a lower mean river gradient than in Districts with a higher gradient when winter rainfall levels were low. The small effect of this interaction generally remained the same through the dataset, except Time Period 2014 when the relative effect noticeably strengthened before being dropped from the model in Time Period 2018 (Fig 2.8E). More detail can be found about these interactions in each Time Period in Appendix 1 (A1.3, A1.4, A1.6). The mean Importance Value assigned to this model term by the model dredging process across the seven Time Periods was 0.42. Although this Importance Value was below the threshold of a moderately important model term, it was included here because of the presence of river gradient, an important variable, within the interaction.

Peatland dominance

Peatland dominance within a District's catchment area was an important positive predictor of the proportional abundance of sea trout in three of the seven Time Periods modelled. Although the strength of the effect size of peatland dominance varied over time, there was no discernible pattern of change across the time series (Fig 2.8G). The small effect size of peatland dominance noticeably strengthened in Time Period 2014 before weakening again in Time Period 2018. The mean of the Importance Values assigned to this model term by the model dredging process across the seven Time Periods was 0.46, indicating that this variable was on the threshold of moderately important.

Percentage of lochs

The percentage of a District's catchment area comprising lochs was an important negative predictor of the proportional abundance of sea trout in three of the seven Time Periods modelled. Although the strength of the effect of the percentage of lochs varied over time, there was a general increase in the strength of the effect across the time series (Fig 2.8H). The small effect of the percentage of lochs within a District noticeably strengthened in the middle of the time series before weakening again in Time Period 2018. More detail can be

found about this relationship for each Time Period in Appendix 1 (A1.3, A1.5, A1.6). The mean Importance Value assigned to this model term by the model dredging process across the seven Time Periods was 0.46, indicating that this variable was on the threshold of moderately important.

2.3.2.3 Rate of change

There were no consistent significant drivers of sea trout population rate of change across the dataset.

2.4 Discussion

It is apparent that sea trout population size is changing with time in different ways in different places (ICES, 2017; Wilson & Veneranta, 2019). A consequence of this variation in population patterns is that there is an increasing need for management strategies that are tailored to specific populations of trout. However, management strategies require an understanding of the historical levels of the population and the factors that are influencing fluctuations in abundance. In most cases, due to a lack of good quality population monitoring data, historical rod catch data is the only available resource that can provide insights to the size of the current population and provide information on previous abundance levels (Crozier & Kennedy, 2001). While it has been argued that rod catch data analysis can lead to the misinterpretation of actual population size (Cowx, 1991), several studies, including a handful that have used the same SSSTF dataset as used in this study, have demonstrated that rod catch data can provide an accurate representation of population change (Crozier & Kennedy, 2001; Youngson *et al*., 2002; Thorley *et al*., 2005). Therefore, we feel that the rod catch data used in this study provides a significant resource that can adequately reflect population changes in Scottish sea trout over the last 67 years.

The SSSTF rod catch dataset was not without some data quality problems, most notably 1) sporadically reported catch returns for some Districts and 2) a lack of distinction between true zeros (no catch of fish) and place holders that represented no catch returns reported. The stringent data selection process used in this study reduced the effect of poor data quality by discarding almost half of the available dataset and only incorporating data where there was a near complete catch records set for the District, therefore providing a high level of confidence in the modelling results.

Based on the rod and line catch data of 64 Districts across Scotland, this study demonstrated that there has been an overall 48% decline in Scottish sea trout populations between 1952 and 2018. There are however important spatial variations in the observed patterns of population change on both a coastal and regional level. Rivers draining to the east of the country showed declines over this period that were considerable smaller (13%) compared with west coast rivers (67%).

This difference could be influenced by several things. For example, Atlantic salmon populations in Scotland have historically dominated in large East Coast rivers, such as the River Tweed. Declines in Scottish Atlantic salmon populations in East Coast rivers (including the Tweed) have been quantified from rod catch data (Youngson *et al*., 2002) indicating that fewer salmon were found in these rivers than had been previously. Declining salmon populations could have a knock on effect on sea trout abundance in these rivers, potentially through reduced inter-specific competition and more habitat available for sea trout to capitalize on. The River Tweed is one of the 13 rivers in Scotland that reported a significant positive rate of change in the number of sea trout that were caught between 1952 and 2018 (Table A1.4), a period over which salmon numbers declined, so it is possible that sea trout populations benefited from this decline. The majority of rivers that showed a significant positive increase in their sea trout numbers were located on the East Coast, potentially indicating a more general effect of reduced intra-specific completion for sea trout. The spatial variation in population change described here differs from results of previous studies that examined changes in salmonid abundance in different geographic locations around Scotland using the same historic dataset used in this study. Youngson *et al.* (2002) determined that seven east coast rivers exhibited high levels of coherence in the temporal and spatial variations in rod catches of Atlantic salmon (*Salmo salar*).

In a non-peer reviewed and self-published preliminary analysis, Jaffa (2018) claimed that sea trout abundances on the East and West Coasts of Scotland were declining at the same rate. The more detailed study presented here showed that both East and West Coasts populations experienced overall declines in sea trout catches, however the West Coast populations suffered a significantly greater and more rapid loss of sea trout (67%) compared to the East Coast (13%) between 1952 and 2018. Similar variations in sea trout population trends have also been reported in England, where there has been an overall national decline in populations. Rivers in the north west of the country, however, showed a decrease in sea trout over the same time period (Harris & Evans, 2017), while rivers in the

north east saw an increase in their returning sea trout in the 1990's and 2010's (Davidson *et al*., 2017). Other countries, such as Norway and Iceland, have reported that their native sea trout catch rates also vary spatially, with populations in different locations demonstrating different rates of change (ICES, 2013; Höjesjö *et al*., 2017).

In addition to quantifying both the large and small scale changes occurring within Scotland's sea trout populations, this study also sought to identify the drivers behind such change using an Information Theoretic modelling approach. Given the overwhelming number of environmental and climatic variables that are capable of influencing sea trout populations, this modelling methodology proved to be a successful method of highlighting common drivers that operate consistently over multiple Time Period models (i.e. periods of apparent population change defined by this study). By identifying these common drivers, the study provides insights into the environmental and climatic variables that are most strongly influencing sea trout trends over time.

However, because some drivers were found to operate only occasionally (i.e. in one or two of the Time Period models), it is possible that a particular variable influencing population change operating over a shorter time period would not have been identified as an important long term driver by this modelling approach. Such variables could suggest a shift in the environment that has not yet been in place long enough to impact longer term sea trout population trends or such variables may be a driver of change that is stochastic in nature. An example of such drivers can be found below.

2.4.1 Drivers of Population Change

Region and river length interaction

In the modelling presented here, the broad geographic area, Region was an important predictor of population size. In addition, river length also consistently predicted population size. However, modelling showed that there was a consistent interaction between these two variables, suggesting a complex interrelationship between them after other variables were accounted for.

In general, longer rivers produced larger populations. There are several possible explanations for this; longer rivers are very likely to have more habitat available to meet the needs of all the life stages of sea trout than smaller rivers; larger rivers may also be

significantly more resilient to change than smaller rivers. However, this effect varied between Regions.

Early in the time series, the effect of larger rivers in most Regions was strong with larger rivers supporting bigger populations. However, the strength of this effect eroded over the time series examined here such that the relative effect of larger rivers was considerably reduced by the end of the time series. This points to an erosion of the resilience of sea trout populations in larger rivers to change with time in some regions. In some Regions, such as the North and North East Regions of Scotland, there was a small effect of river length in the opposing direction, suggesting that the positive effect of large rivers is not universally applicable.

From 2000 to 2018, there is less variation in the predicted sea trout populations in different Regions, indicating that sea trout catches from most Regions are becoming more similar to each other and, in some cases, are at much lower levels relative to what was historically caught. This is mostly because Regions with higher historical catches are declining more rapidly, with Regions with historically lower catch declining less rapidly, eroding the historical difference in catches between Regions. The homogenization of predicted sea trout populations across Regions indicates that some historically resilient populations in Scotland, such those found in the Solway Region, are now less able to maintain that resilience.

Winter rainfall and river length

Another strong driver of sea trout population size after other variables were accounted for was mean monthly winter rainfall. High winter rainfall ultimately had a negative effect on sea trout populations, but its effect size decreased over time. Thus from 1966 to 2000, winter rainfall was an important predictor as an effect on its own. From 2000 to 2018, this effect was no longer highly important on its own, but instead became a highly important predictor for sea trout catch when included in an interaction between winter rainfall and river length.

This shift in the way that winter rainfall influenced sea trout populations to include river length suggested that historically, regardless of river size, sea trout population size was depressed by heavy winter rains. Later in the time series (after 2000), although sea trout populations across all river lengths continued to show declines during high winter rainfall, the magnitude of the effect populations was related to river length.

The finding that sea trout populations are declining when winter rainfall increases could be due to a variety of factors. Increased winter rainfall can lead to extreme flooding and ultimately juvenile fish strandings or direct mortality and redd washouts which may affect population size (Jonsson & Jonsson, 2009b). Furthermore, overgrazing and development of riparian zones leads to the degradation of freshwater habitat as the water quality and structural stability of river banks is affected (Hendry *et al*., 2003). This in turn inhibits a river's ability to buffer heavy rainfall and can lead to further flooding.

Mean river gradient

The mean river gradient of a District was an important positive predictor of sea trout populations. This relationship indicated that higher sea trout levels were being reported from rivers having a steeper mean river gradient after other variables were accounted for. This strong effect may well represent the abundance of high quality habitat available for sea trout. The majority of rivers with a high mean gradient are found on the West Coast of Scotland, either on the islands or in the north-west of mainland Scotland. This is consistent with the general mountainous topography of these areas, where rivers are often shorter and steeper and generally understood to provide good habitat for sea trout populations. This contrasts with longer, more southern rivers, with a lower gradient where the majority of available river habitat may well be better suited to Atlantic salmon.

It is possible that a mechanism similar to that operating in high gradient catchments could also be operating in rivers with high peatland dominance and a low percentage of calcareous geology. These three environmental characteristics (high gradient: high peatland dominance: low percentage of calcareous geology) often overlap in Scottish geography, most commonly in the northern half of the country. Such catchments are recognized for their ability to support brown trout populations when other fish species, including salmon, are not as abundant because the habitat is not as productive as some larger southern rivers (Frost & Brown, 1967; Campbell, 1971).

Modelling revealed an important interaction between river gradient and winter rainfall and its effect on the number of sea trout caught as a proportion of all fish caught in Scotland in any year. For two periods, 1978 to 2000 and again from 2008 to 2014, this interaction was an important predictor of the size of a population relative to estimates of the national population size. The positive effect of river gradient on sea trout population size was counterposed by a negative effect of winter rainfall. Thus, the relative sea trout population

size in rivers with a lower mean gradient were less affected by the negative effect of high winter rainfall than rivers with a higher river gradient. Conversely sea trout populations in rivers with a higher gradient were more affected by the negative influence of high winter rainfall. The possible mechanism through which this effect may occur is likely to be through an elevated spate effect of high rainfall on high gradient rivers where water velocity and discharge is inevitably higher in steep gradients. This may well affect sea trout populations through redd washout or direct physical effects on overwintering sea trout fry or parr (Jonsson & Jonsson, 2009b).

Solid geology

Another consistent predictor of sea trout population size was the percentage of solid geology within a catchment. Solid geology, which was derived in this study from a Scottish Environmental Protection Agency dataset (SEPA, 2019), is defined as the percentage of solid geology (bedrock) at the surface in the catchment. The alternative to solid geology in a catchment is drift geology, a term encompassing a wide variety of materials (gravel, silt, clay, etc.) that were deposited in catchments during the Quaternary glaciation (Fairbridge, 1968). Given the consistent negative relationship between the percentage of solid geology within a District and sea trout populations, it is clear that this study supports the findings of previous research that demonstrate that high percentages of drift geology are beneficial to trout populations (Armstrong *et al*., 2003). River systems that are comprised primarily of bedrock provide little to no usable habitat for trout populations as they are often fast flowing with little nutrients available, providing poor invertebrate habitat and little cover from elevated temperatures or predators (Palm *et al*., 2006). In contrast, the variation in river substrate that often accompanies drift geology is more likely to support varied habitats supporting a greater variety of aquatic flora and fauna. Catchments with a high percentage of drift geology are, for example, likely to support habitats that might include gravel for spawning adults and sections of slightly larger substrate such as pebbles and cobbles that are better suited to the juvenile stages of sea trout (Jonsson & Jonsson, 2011).

Peatland dominance

Peatland dominance was determined to be a highly important positive predictor of sea trout populations in 57% of models when other variables were accounted for. Rivers with high peatland dominance are primarily found spread across the northern half of Scotland, which may well be inherently more suited to trout than salmon therefore potentially reducing inter-specific competition. Rivers with the lowest levels of peatland are located primarily

in the southern half of the country, however there are a few exceptions that are found further north. The positive effect of peatland dominance on sea trout populations increased from 1952 to 2000, after which it declined. This decline in effect could represent a decline in the amount of organic material available along the riverbank due to threats such as overgrazing.

The mechanism through which the percentage of peatland in a catchment may positively influence sea trout populations is unclear. One possibility is that catchments with high peatland dominance are less suitable as habitat for competing Atlantic salmon and thus are more likely to support higher sea trout populations.

Water pH can be influenced by the presence of peatland, depending on the type of peat or its stage of development, however, in areas of high peatland dominance, water pH tends to be more acidic (Craft, 2016). Frost & Brown (1967) reported that Scottish freshwater catchments with a high peat percentage are capable of supporting trout populations but not many other species. While it is ideal that there are catchments in Scotland that trout populations can monopolize, rivers in areas with a high presence of peatland dominance can also be nutrient poor (Craft, 2016), which could result in high levels of intra-specific competition between trout populations. This level of competition has been shown to increase the likelihood of an individual trout migrating to sea (Chapman *et al*., 2012). Therefore, it could be expected that young trout in areas of high peatland dominance are encouraged to activate their migratory phenotype instead of remaining in their natal river. However, this explanation is rather speculative; this relationship is worth of more research attention.

Calcareous geology

The percentage of calcareous geology with a District's catchment was determined to be a moderately important negative predictor of the proportional abundance of sea trout populations in 57% of models when other variables were accounted for. The effect of calcareous geology was particularly strong between 1952 and 1966, weakened from 1966 until 2000, and then increased in strength again from 2000 to 2018. This negative influence was unexpected given that chalk streams in England are well known for their productivity and rich biodiversity (Mann *et al*., 1989). Rivers with a high percentage of calcareous geology were primarily located in either the Clyde or West Regions while the rivers with the lowest percentages of calcareous geology were primarily found in the Solway Region.

Calcareous geology is often associated with a more alkaline pH. Rivers with a high water pH are known to support a wide variety of different types of fish, however Scottish catchments with soft water, or a low pH (often associated with peatland), are more likely to support populations of trout, but very few other species (Frost & Brown, 1967). As such, there are at least two possible mechanisms through which a productive catchment with a high percentage of calcareous geology and accompanying productive and diverse communities may influence sea trout population size. Firstly, if there are enough resources and habitat available, the juvenile trout may not make the decision to migrate to sea and therefore remain in the freshwater catchment as freshwater-resident brown trout, not sea trout. An alternative explanation is that juvenile trout populations when faced with a high level of interspecies competition are not as productive in freshwater causing them to migrate where they face additional mortality at sea resulting in lower population size (Montorio *et al*., 2018).

Because the SSSFT dataset does not include freshwater resident brown trout catch records, it was not possible to test the first of these speculative explanations to determine if there was a trade off in polymorphic life history strategies implemented in rivers with opposing alkaline and acidic pH values.

Percentage of lochs in a catchment

This study determined that the percentage of a catchment comprising standing water (lochs) was important in predicting the proportional abundance of sea trout. Rivers comprising a greater percentage of freshwater lochs in the catchment made up a relatively smaller percentage of the total sea trout in Scotland when other variables were accounted for. The majority of the rivers with the highest percentage of lochs were scattered across the West, North West, and Outer Hebrides Regions. One possible explanation for this finding is that these catchments are supporting greater populations of resident brown trout because the catchments are able to provide adequate habitat space and nutrients in their freshwater systems which could influence the trout's decision to remain in freshwater.

Sea temperature

An example of a driving factor that was only operational for a short period of time was the significant relationship between the rate of change of sea trout populations and the polynomial term of sea temperatures from 2000 to 2008 (Table A1.10). The data subset of the Time Period model reported the highest sea temperatures to be included in this time series, with temperatures ranging between 10.1°C and 12.1°C from 2000 to 2008. During

this time, sea trout populations demonstrated a positive increase in the rate of population change as temperatures rose from 10.0°C to around 11.0°C; at sea temperatures beyond 11.0°C, however the rate of change began to decline.

Because this relationship was only reported to be highly important for this measure of abundance change over a short period of the overall dataset, it was not a consistent driver of long term population change. However, this effect may be more important in the future. As sea temperatures continue to increase due to climate change (Townhill *et al*., 2019), this variable could have a more consistent and, negative effect if temperatures consistently exceed 11 C°, on the rate of change in sea trout populations.

Please see Appendix 1 for examples of other variables that were important in individual Time Period models but not throughout the dataset.

2.4.2 Broad Themes

This study has demonstrated the Information Theoretic modelling techniques used here are capable of identifying multiple variables that act as predictors of long term Scottish sea trout population change. To our knowledge, this is the first time such a study has identified driving variables behind long term sea trout populations trends across Scotland.

Because the study has determined how sea trout populations have reacted to these variables in a historical context, it is possible to predict how the populations would be impacted as variables change in the future. A pertinent example of this are the effects of climate change on sea trout populations. This study demonstrated that in the last two decades, climatic variables such as sea temperature and winter rainfall are generally increasing and likely to increase further, and are having stronger negative impacts on various measures of sea trout abundance than they had in previous years. Warmer sea temperatures and more extreme weather events that coincide with heavy rains are becoming more frequent around the world (Townhill *et al*., 2019). As these environmental conditions change, one strong conclusion resulting from the findings of this study is that Scottish sea trout, and most likely other European trout populations, will experience declines as a result.

In this study, a number of predictors of sea trout abundance relate directly to the catchment of origin of the sea trout population. Thus, the percentage of the catchment comprising

percentages of solid geology and calcareous geology (both negatively), peatland dominance (positively), river gradient (positively) and the percentage of standing water in the catchment (negatively) all have an effect on the sea trout population size. These features are largely fixed attributes of the catchment and mostly invariant over long time periods. It is these features that are likely responsible for much of the spatial variation at coastal, regional and catchment scales described in this study.

For a number of apparently invariant characteristics of a catchment, their effects on sea trout populations have changed with time. The observed effect is not demonstrating a change in the invariant characteristic itself, but rather is reflecting the change in the resilience of sea trout populations in catchments with those characteristics relative to changes in other fluctuating variables, such as rainfall. For example, river gradient of a catchment area will not have been altered over the course of six decades, however, as winter rainfall levels and intensity have increased over time, catchments with a high river gradient would be more susceptible to flash flooding and redd washouts, leading to a decline in sea trout abundance.

River length (which is unchanging over the time period of this study) predicted sea trout population size at the beginning of the timeseries. Thus, longer river supported larger populations. However, its effect was eroded with time such that by 2000 the effect of river length had been minimized in regions where this effect was greatest. Why this effect has now been lost is uncertain but one possibility is that a presumptive resilience of larger rivers to change in sea trout population size has been eroded over the last two decades.

Another important driver of sea trout population size that has changed over time is winter rainfall. This variable had significant effect on population size in between 1966 and 2000. However, the strength of this effect increased with time (up to 2000) after which it declined again. Winter rainfall is predicted to continue increasing in Scotland in the future under current climate change models (Hurrell *et al*., 2003; Boylan & Adams, 2006) suggesting that this negative impact on sea trout populations is only going to become more acute. This negative effect may be further enhanced by the effect of river gradient. River gradient in general positively predicted sea trout population size but there was a strong interaction between river gradient and winter rainfall, thus the impact of winter rainfall was greater in high gradient rivers, the river types which were more likely to support larger sea trout populations; thereby increasing the negative effect of winter rainfall. The data presented here strongly points towards those drivers of change that are temporally labile

continuing to exert negative pressure on sea trout populations under most scenarios for climate change effects on rivers.

Although this study examined the effects of a number of potential drivers of sea trout population change, there are certainly others that were not included in the analysis because data was not readily available. Using a similar study design, future analysis could include potential drivers such as trends in marine fishing pressure, changes in land use and expansion of marine development.

Chapter 3: Influences of open net-pen aquaculture on anadromous sea trout (*Salmo trutta*) populations on the west coast of Scotland over the last 20 years

Abstract

Open-net pen Atlantic salmon aquaculture is one of the largest and fastest growing industries on the west coast of Scotland, but there are several impacts of intensive aquaculture that can negatively impact wild sea trout populations. Despite the well-researched recognition of these industry effects, there has been little attempt to quantify their impact on long term trends of sea trout populations. The study presented here used Information Theoretic modelling to analyse a 17 year dataset (2002 to 2018) comprising rod catches from 47 catchments across the west coast of Scotland to show patterns of change and to identify environmental, climatic and aquaculture drivers of these changes over time.

From this analysis, Scottish sea trout population size trends are different in areas with and without open-net pen Atlantic salmon aquaculture and these responses are strongly influenced by additional climatic and environmental drivers. Furthermore, in areas were open-net pen aquaculture is present, sea trout populations are impacted by increasing biomass production but the strength of this effect was also driven by further climatic and environmental drivers.

Sea temperature, winter rainfall and river length were found to be particularly important predictors of sea trout populations when combined with aquaculture variables. River length had a positive effect on sea trout populations when aquaculture facilities were not present, but when open-net pens were located within 30 km of a river, longer rivers suffered greater declines in sea trout populations as pen biomass increased. As annual mean sea temperature increased above 11°C, the negative effects of open-net pens on sea trout populations were exacerbated. Years of heavy winter rainfall were found to benefit sea trout populations in areas of aquaculture, possibly a resulting effect of decreasing salmon lice abundance in areas of low salinity.

Given the high likelihood that climatic variables will experience changes in the future due to modelled climate change shifts, and the projected expansion of Atlantic salmon

aquaculture in Scotland, it is suspected that these complex relationships will have an even larger negative impact on sea trout in future years.

3.1 Introduction

Aquaculture is one of the fastest growing food sector industries in the world, producing a wide variety of different aquatic flora and fauna, including crustaceans, molluscs, seaweed and finfish for human consumption and various other uses (FAO, 2019; Atalah & Sanchez-Jerez, 2020). The aquaculture industry globally produced 53.4 million tonnes of finfish (worth an estimated USD 139.7 billion) in 2017 (FAO 2019). Of that, 2.3 million tonnes comprised Atlantic salmon (*Salmo salar* L. 1758). The largest Atlantic salmon producers are Norway, Chile, and Scotland (OECD, 2020).

Atlantic salmon aquaculture began in Scandinavia and the UK in the late 1960's and early 1970's (Taranger *et al*., 2015; Thorstad *et al*., 2015; Shephard *et al*., 2016). The majority of Atlantic salmon aquaculture occurs in open-net pens (hereafter referred to as net-pens) located in coastal marine areas (Ford & Myers, 2008). Several negative environmental impacts of this type of aquaculture have been identified as the industry has expanded, including the degradation of the seabed and water quality around the net-pens, as well as the impacts of salmon escapees on native salmonid populations (Green *et al*., 2012; Gonzalez & de Boer, 2017; Atalah & Sanchez-Jerez, 2020).The impact that has evoked the most concern however, is the potential for the transfer of pathogens from salmon in coastal net-pens to wild salmonid populations that utilize the same areas. One parasite, the copepod crustacean, *Lepeophtheirus salmonis*, hereafter referred to as the salmon louse, is of particular concern (Shephard *et al*., 2016; Thorstad & Finstad, 2018).

The salmon louse is a naturally occurring parasite in the marine environment that generally appears on wild salmonids in low numbers, resulting in few negative impacts on their hosts (Thorstad & Finstad, 2018). However, at high densities, salmon lice can cause severe damage to fish, including skin and tissue damage, osmoregulatory stress, increased susceptibility to predation and ultimately increased mortality (Thorstad *et al*., 2015).

Research has demonstrated that by the 1980's when the industry began to significantly expand, salmon aquaculture net-pens were often linked with increased salmon lice levels in the surrounding water column (Ford & Myers, 2008; Torrissen *et al*., 2013; Thorstad *et al*., 2015). In net-pens where there are large numbers of hosts, salmon louse densities can reach high levels if left untreated (Rogers *et al*., 2013). Lice can be carried from the net-pens by tidal and wind driven currents into the surrounding environment where wild

salmonids come into contact with them (Thorstad *et al*., 2015). Middlemas *et al*. (2013) and Rees *et al*. (2015) both reported increased levels of salmon lice in the water column for up to 30 km away from net-pen salmon aquaculture sites.

This far-reaching influence of net-pens is thought to have a large impact on wild anadromous *Salmo trutta* L. 1758 (hereafter referred to as sea trout) which are known to frequently utilise foraging grounds in the same coastal zones that are used for salmon aquaculture (Shephard *et al*., 2016). As with all migration strategies, anadromous sea trout accrue benefits (increased feeding opportunities and therefore larger growth rates) as well as costs (increased predation, pathogen exposure and mortality) by moving into the marine environment. The magnitude of each of these costs is not fully understood, however the impact of salmon aquaculture on these populations is thought to be relatively high in intensive aquaculture areas. Several studies have demonstrated that this overlap in habitat use leaves sea trout, particularly young sea trout, vulnerable to increased levels of salmon lice infections which can lead to increased mortality (Aldvén & Davidsen, 2017; Moore *et al*., 2018; Thorstad & Finstad, 2018; Serra-Llinares *et al*., 2020).

Net-pens are found across the northern and western coasts (but not the east coast) of Scotland. Commercial salmon aquaculture began in Scotland in the 1960's and has expanded rapidly over time (Ellis *et al*., 2016). Annual Scottish reported production showed a 91% increase in the tonnage produced between 1997 (99,197 tonnes) and 2017 (189,707 tonnes) (Fig 3.1) (Munro & Wallace, 2018) and Scottish Government policy is to increase this to 210,000 tonnes by 2020 (Kenyon and Davis, 2018).

Sea trout populations across Scotland have been shown to have declined by 48% in the last 67 years (Moore *et al*. in prep; Chapter 2). However, sea trout populations in rivers draining to the west coast of the country have been shown to have declined at a much faster rate (67% in 70 years) compared with those in rivers on the east coast (13%) over the same period (Moore *et al*. in prep; Chapter 2). Although it is clear that there are other driving forces that have influenced this decline (Moore *et al*. in prep; Chapter 2) and other potential drivers of change that have not been fully tested (e.g. predation, exploitation, climate change) the development of net-pen salmon aquaculture and it subsequent influence on the marine environment has been implicated as a significant contributing factor in the decline in sea trout numbers on the west coast of Scotland through increased salmon lice infections (Penston & Davies, 2009; Middlemas *et al*., 2013; Shephard *et al*., 2016; Moore *et al*., 2018).

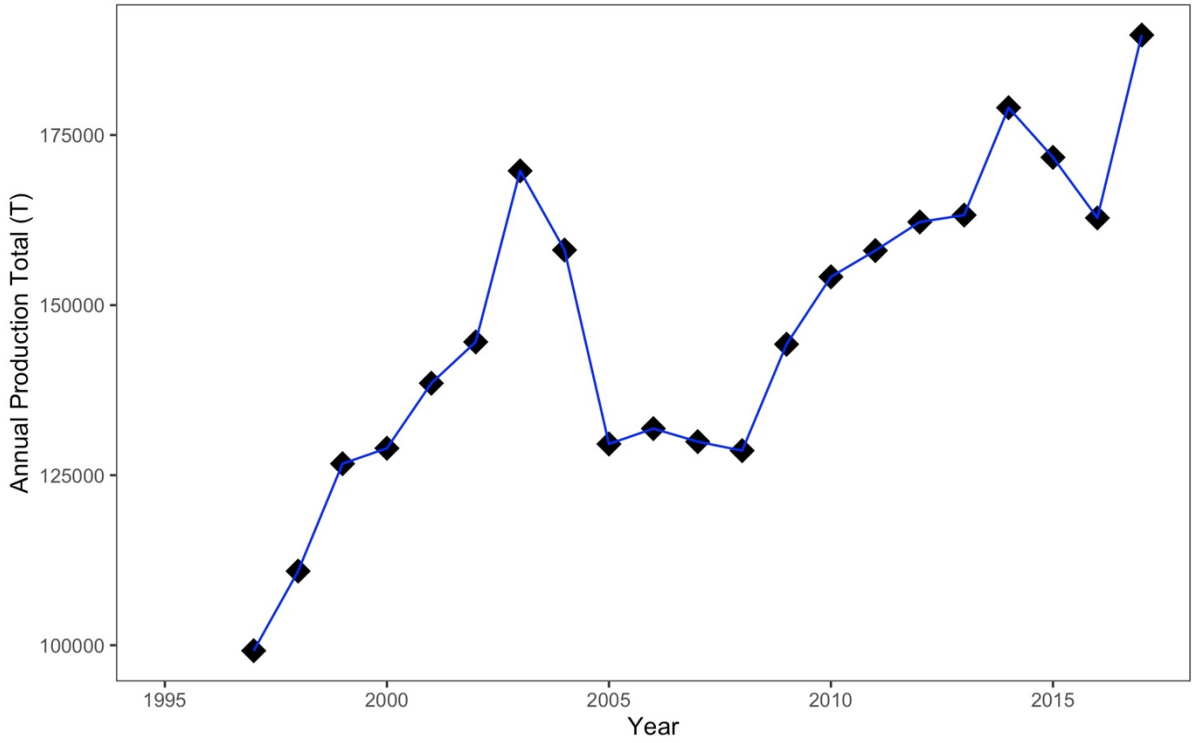


Figure 3.1. Annual production total (T) of Atlantic salmon in the Scottish aquaculture industry (1997-2017). Data from the Scottish Fish Farm Production Survey 2017 (Munro & Wallace, 2018).

Previous studies have demonstrated short term effects of salmon aquaculture on sea trout on the west coast of Scotland. To date, no research has been conducted to test the potential longer term effects on populations. The study presented here seeks to identify any possible influence that Atlantic salmon aquaculture might have on long term sea trout population trends in Scotland over the last 20 years.

In this study we test two specific hypotheses:

(1) Does the presence of net-pen salmon aquaculture influence the population size of sea trout on the west coast of Scotland?

(2) When net-pen salmon aquaculture is present, does the annual maximum biomass of each net-pen facility influence sea trout population size?

3.2 Materials and Methods

To determine the temporal patterns of sea trout population change and to explore potential drivers of population change over time in relation to the development of net-pen salmon aquaculture, here we use net-pen biomass data, as well as climatic data and small and larger scale environmental data as putative predictors of the sea trout population size in an Information Theoretic modelling analysis (Grueber *et al.*, 2011) (Table A2.1). An essential precursor to model construction is data selection and rationalisation.

3.2.1 Data Sources and Rationalisation

3.2.1.1 Sea trout population size data

There is a large, publicly available, historical dataset of catches of Scottish Atlantic salmon and sea trout from 1952 to the present (Marine Scotland, 2019). There is a statutory requirement for annual returns of all Atlantic salmon and sea trout catches from both commercial and recreational fisheries in Scotland to be made to Scottish Government. Freshwater-resident brown trout catches (despite also being *Salmo trutta*) are not required (Marine Scotland, 2015).

This dataset, the “Scottish Salmon and Sea Trout Fishery Statistics” (hereafter the SSSTF dataset), comprises the reported numbers of salmon and sea trout captured in 109 “Districts” from three different capture methods, two primarily commercial, coastal and estuarine methods (although some records come from freshwater systems) (called “fixed engine” and “net and cobble” fishing), and one recreational (rod and line). In 1994, an additional capture category was introduced to the dataset to separate the number of sea trout that had been captured by rod and line but released from those that were captured and retained. In 2004, a separate category for captured finnock (sea trout weighing less than 0.5kg) (Marine Scotland, 2015) was created in addition to adult sea trout catches.

Historically, commercial netting was not conducted in all catchments across Scotland and commercial netting for salmonids has declined markedly over the period of this dataset. Thus, commercial net capture data are temporally and geographically skewed; for this reason, we follow the logic of Youngson *et al.* (2002) and used only rod and line catch data in the study presented here. Youngson *et al*. (2002) rationalized that rod catches provided an accurate depiction of salmon abundance trends at an individual catchment level, and used the SSSTF dataset (used in the study reported here) to investigate trends of multi-sea winter (MSW) salmon from 1952 to 1997.

The SSSTF dataset does not provide any measure of fishing effort for the rod fishery (Marine Scotland, 2015). However, rod catch data, uncorrected for effort, has been shown to be a good index of population size. For example, in the UK, several studies have shown strong linear relationships between rod catch data of Atlantic salmon and data derived from fish counters installed in the same rivers (Beaumont *et al*., 1991; Crozier & Kennedy, 2001). In British Columbia, regional variation in fishery-dependent measures of populations of steelhead trout (*Oncorhynchus mykiss*) abundance has shown similar trends to data from fishery-independent methods (Smith *et al*., 2000). Thorley *et al*. (2005) compared Atlantic salmon rod and line catch data from the SSSTF dataset with counts from fish counters in 12 Scottish rivers and showed similar trends between the two methods.

Thus, we argue that rod catch data generally, and for the SSSTF data specifically, even if not corrected for fishing effort, can be successfully used to analyse the spatial and temporal abundance trends in sea trout in Scotland.

3.2.1.1.1 Data quality control and improvement

Sea trout and finnock have been recorded separately in the SSSTF dataset since 2004; for the purposes of this study, annual catches of both were combined for further analysis. Additionally, in this study the returns sea trout caught and killed and caught and released were also similarly combined.

A total of 106 reporting "Districts", comprising either single catchments or several neighbouring catchments, reported sea trout rod and line catch data in the SSSTF dataset. Of these 106 Districts, 76 were located on the west coast and 30 were located on the east coast. For the purposes of this study, only 76 Districts comprising rivers that drained to the west coast of Scotland were considered for the analysis (as there is no net-pen salmon aquaculture on the east coast) (Fig 3.2A).

To improve data quality and reduce missing data (Grueber *et al*., 2011), 22 Districts that did not have a full catch record history in the dataset were removed from the dataset. Zero (0) entries to the SSSTF dataset comprised two different types of data: a catch return where no sea trout were captured in that year and where there was no catch return made for that year. Unfortunately, it is not possible to distinguish between these two zero entry types (Marine Scotland, 2015). Districts with records comprising 25% or more zeros across all years were removed from further analysis (6 Districts removed). Thus, a subset of data from 48 Districts remained. The 2002-2018 catch records of these 48 Districts were used in the statistical analysis to coincide with an available aquaculture dataset.

These data were then used to generate three metrics of sea trout population size for each year, for each District separately (Table A2.1).

1. **Sea trout catch**- was determined as the actual reported rod catch of sea trout for that District for each year.
2. **Proportional abundance**- was calculated as the actual annual reported rod catch for that District expressed as a proportion of the total catch from all 48 Districts combined for that year. This metric gave a measure of the relative contribution of that District to the west coast rivers catch for that year. To meet normality assumptions, proportional abundance was square root transformed.
3. **Rate of population change**- was calculated as the gradient of a single District's rod catch regressed on time (in years) over a defined period. In order to meet model normality

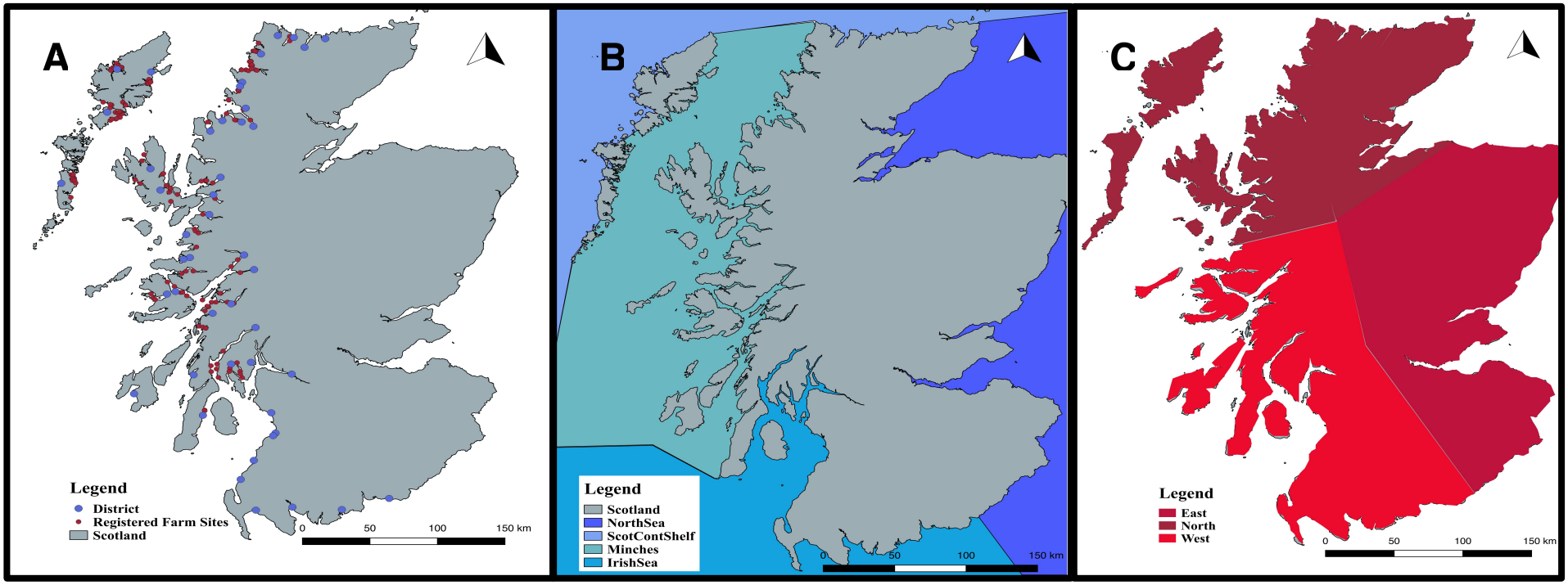


Figure 3.2A-C. Map panel of specified geographic areas used in this study. a- Map of Districts (N=47) and registered open-net pen aquaculture sites within 30km of the Districts as of 2018. Aquaculture data from Scotland's Aquaculture Database (Scottish Government, 2018); b- sea temperature (C°) zones (N=3; as no Districts were located in the "North Sea" zone, no data from that area was used in this study); c- rainfall (mm) and air temperature (C°) zones (N=2; as no Districts were located in the "East" zone, no data from that area was used in this study).

assumptions, this metric was then scaled by subtracting the mean of the dataset from each value and then dividing by the standard deviation.

3.2.1.2 Environmental data

A key element of Information Theoretic modelling is the use of model terms that are likely to be ecologically relevant (Grueber *et al*., 2011). To identify potential drivers of change in sea trout populations, a number of environmental variables with the potential to affect sea trout were identified. The logic for the inclusion of each is presented in Table A2.1. In the first stage of this analysis, ecologically relevant and available environmental data were separated into three categories: River specific environmental data, Climatic data and Aquaculture data. The ranges of each variable can be found in Table A2.1.

3.2.1.2.1 River specific environmental data

River specific data were collated for each District from the Scottish Environment Protection Agency (SEPA) "River and loch waterbody nested catchments" dataset (SEPA, 2019). River specific data are available for individual sections of rivers and lochs (hereafter referred to as "segments") that make up a complete catchment. The data from all of the segments within a catchment were combined together to generate District specific data (calculations for each river specific variable are outlined in Table A2.1). The percentage of lochs within a District was calculated by dividing the SEPA reported total surface area of freshwater lochs within a catchment by the total area of the catchment (Table A2.1).

For those Districts comprised of a number of neighbouring catchments (Loch Long, Loch Roag, Little Loch Broom and Fincastle Districts) where multiple rivers discharged into a common coastal zone, the data for all of the freshwater catchments flowing into that coastal zone were included in the overall dataset for that District.

One District (Inner District; Isle of Jura) had to be removed because river specific data could not be confidently identified. Thus 47 Districts were analysed further (Table 3.1).

Nine river specific environmental variables selected from the SEPA dataset were chosen for their "ecological relevance": river length, maximum river altitude, mean river gradient, the number of combined sewer overflows (CSO) per km in the district, the percentage of

Table 3.1. List of the 47 Districts included in this study. Districts with active net-pen facilities within 30km are highlighted in **bold**.

River	Aquaculture	River	Aquaculture
Arnisdale	**Present**	Annan	Absent
Awe	**Present**	Ayr	Absent
Baa	**Present**	Clyde	Absent
Broom	**Present**	Cree	Absent
Carradale	**Present**	Doon	Absent
Carron	**Present**	Girvan	Absent
Creed	**Present**	Irvine	Absent
Echaig	**Present**	Kinloch	Absent
Ewe	**Present**	Laggan	Absent
Fincastle	**Present**	Luce	Absent
Fyne	**Present**	Naver	Absent
Grudie	**Present**	Nith	Absent
Gruinard	**Present**	Stinchar	Absent
Hope	**Present**	Urr	Absent
Howmore	**Present**		
Inver	**Present**		
Kanaird	**Present**		
Kirkaig	**Present**		
Laxford	**Present**		
Leven	**Present**		
Little Loch Broom	**Present**		
Loch Long	**Present**		
Loch Roag	**Present**		
Lochy	**Present**		
Moidart	**Present**		
Morar	**Present**		
Nell	**Present**		
Ormsary	**Present**		
Pennygowan	**Present**		
Ruel	**Present**		
Shiel	**Present**		
Sligachan	**Present**		
Snizort	**Present**		

the catchment within a 1:10 year predictive flood area, the percentages of calcareous, peat and solid geology within a catchment, and the percentage of loch (standing freshwater) surface area in a District (Table A2.1).

3.2.1.2.2 Climatic environmental data

Climatic environmental data were collated from several sources.

The North Atlantic Oscillation index (hereafter referred to as NAO) reports the quantitative changes in sea-level pressure between the Azores and Iceland and is a reputable source of atmospheric variability (Sarafanov, 2009). In the UK, positive NAO values represent mild, stormy weather events, while negative NAO values indicate cold, calm weather. Previous studies have demonstrated that fluctuations in NAO values can be linked to changes in environmental conditions that salmonids are exposed to in the marine environment, making NAO an important variable to consider in a long-term time series analysis (Honkanen *et al*., 2018). Annual mean NAO data were derived from a historical dataset updated annually by the University of East Anglia (Climate Research Unit, 2019).

Annual mean sea temperature data for three regions around Scotland were taken from the Scottish Ocean Climate Status Report (Hughes *et al*., 2018) (Fig 3.2B). Districts were assigned a sea temperature based on their location in one of those three regions.

Annual rainfall and air temperature data were derived from the UK Meteorological Office data (Met Office 2019). Region specific data for both rainfall and air temperature were assigned to each district based on their geographic location within the two regions (Fig 3.2C).

Mean seasonal values of rainfall and NAO were separated into mean summer and winter categories. For both of these variables, a summer value was generated by calculating the mean from values reported between April in Year X to September in Year X. A winter value was generated by calculating the mean from values reported between October in Year X to March in Year X+1. The standard deviations of seasonal rainfall were also calculated as a measure of the fluctuations around both summer or winter rainfall means.

All climatic variables were also modelled as second order polynomials because extreme periods of drought or heavy precipitation may have negative impacts by exceeding the optimum ranges for trout (Armstrong *et al*., 2003).

Thus, twelve climatic variables were chosen for their ecological relevance: the linear and second order polynomial of mean sea temperatures, mean winter rain, mean summer rain, mean winter NAO, mean summer NAO, as well as winter rain variance and summer rain variance (Table A2.1).

3.2.1.2.3 Aquaculture data

In addition to the environmental variables described above, the location of registered net-pen Atlantic salmon aquaculture sites in Scotland and net-pen biomass data were collected from the Scotland's Aquaculture Database (Scottish Government, 2019).

In order to test for any potential effect of net-pen facilities on sea trout populations, two net-pen metrics were determined. Previous research has demonstrated that in Scotland, increased lice levels from net-pens can be found up to 30 km away from the nearest site (Middlemas *et al*., 2013; Moore *et al*., 2018). Firstly, a binomial "Present" or "Absent" value was assigned to each District based on the presence of net-pens within 30 km of the District's main river mouth. The distance between a District and a net-pen site was measured from the mouth of the main river in the District, or in the cases of Loch Long and Loch Roag, from the centre of the sea loch into which all local freshwater catchments discharged. Distances were measured as the shortest route by sea.

Secondly, the cumulative biomass of a net-pen facility within 30 km radii of the river mouth for each District (or the sea loch centre for Lochs Roag and Long) was determined.

3.2.1.3 Variable selection

Once all of the ecologically relevant environmental variables had been selected, they were then tested for collinearity (see below) (Cade, 2015; Zurr *et al*., 2015). For variables that were highly correlated (>0.7), a single variable that was determined to be the most ecologically relevant, was included for further analysis and all remaining correlated variables were removed from analysis to avoid replication of variation.

Before modelling began, all selected independent environmental variables were scaled by subtracting the mean of the dataset from each value and then dividing by the standard deviation.

3.2.2 Modelling the Potential Effects of Salmon Aquaculture

3.2.2.1 Information Theoretic modelling

Information Theoretic modelling is a useful modelling method for ecologists because of the robust nature of model selection (Katsanevakis & Maravelias, 2008; Ianellie *et al*., 2016; Walker, 2017). More traditional hypothesis testing is limited by step-wise model selection and the use of AIC units to identify the best model explaining variation; it can often result in several models with very similar AIC values (Grueber *et al*., 2011). In these circumstances, the simplest model of the group is often chosen as the best representative of the relationships in question, however, this method has the potential to eliminate important nuances of independent variables that might be explained by more complex models (Symonds & Moussalli, 2011).

The Information Theoretic approach combines models which are not easily distinguished statistically, by averaging model terms across all models within two AIC units (Grueber *et al*., 2011; Harrison *et al*., 2018). A second advantage of this approach is that model terms are selected through ecological reasoning using the system being investigated (Katsanevakis & Maravelias, 2008). In the study presented here, the variables included in the Information Theoretic modelling approach were thus chosen for their relevance as potentially impacting upon salmonid populations.

3.2.2.2 Overview of modelling process

The development of a final model using the Information Theoretic model was a 5 step hierarchical process (Fig 3.3). These steps were:

1. Variable selection: To avoid overfitting the final model, variable selection was undertaken for each of the two categories of explanatory variables (River specific and Climatic). For each variable category, each of the three sea trout population metrics (sea trout catch, proportional abundance, and rate of population change) were regressed on the independent group variables separately.

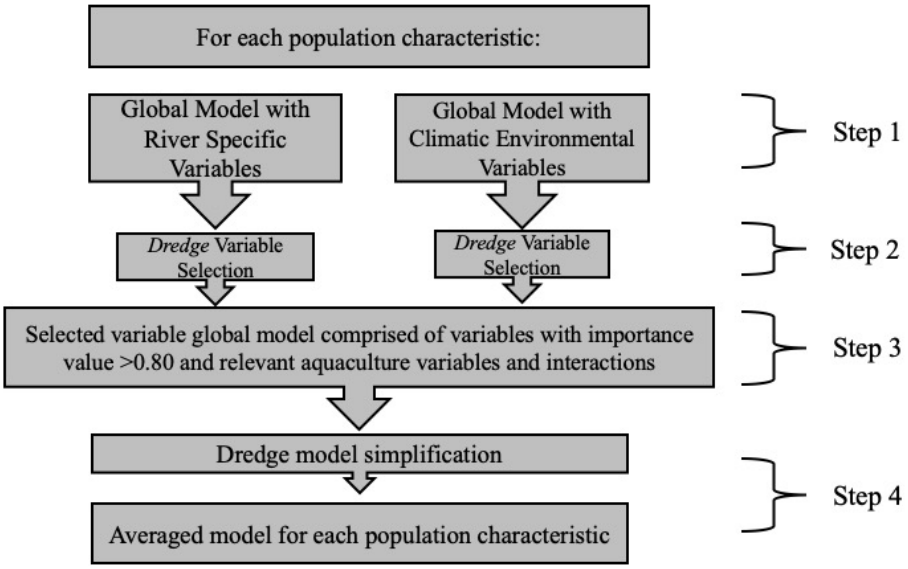


Figure 3.3. Flow chart outlining an overview of the Theoretic Information modelling process

2. Variables from each category were identified for further consideration using the "*dredge*" function in the R package MuMIn (Barton 2019). Variables which appeared in 80% or more of all possible models within 2 AIC units of the model with the lowest AIC value (i.e. a 0.8 model term "Importance Value" *sensu* Grueber *et al*., 2011) were considered further. Model term Importance Values range between 0.00 (i.e. the variable appeared in none of the models that fall within 2 AIC units of the model with the lowest AIC value) and 1.00 (i.e. the variable appeared in all of the models that fall within 2 AIC units of the model with the lowest AIC value).
3. All variables selected at Step 2 (from the two environmental categories) and aquaculture variables were entered in a global model that combined variables from all groups and their interactions.
4. Model averaging was used to produce a final model describing the changes in sea trout population characteristics based on the variable selection process (Steps 1-3). Using the *dredge* function, all models within 2 AIC units of the lowest ranked model were averaged (a full average *sensu* Grueber *et al*., 2011) to produce a final averaged model. Model terms that were assigned an Importance Value of >0.80 were defined as highly important, while terms that were assigned an Importance Value of 0.50-0.80 were defined as moderately important (Grueber, *et al*. 2011).
5. Each step was repeated separately for each of the three metrics defining sea trout population characteristics (sea trout catch, proportional abundance and rate of population change).

These initial models (Step 1) included both the fixed effects of all environmental variables and the second order polynomial terms of climatic variables. Using the *dredge* command from the package MuMIn (Barton, 2019), all possible model combinations were investigated to construct a final averaged model (Step 4; Fig 3.3) that combined all the models within two AIC units of the lowest AIC value assigned to a model. If a model term was included in the global model (Step 3) but was not present in the final averaged model (Step 4), it was dropped during model averaging because it did not appear in the models within 2 AIC units of the lowest ranked model (Grueber *et al*., 201). This is denoted in future tabular results by the text "Dropped".

The fit of each environmental variable group model was determined by assessing the regression of the modelled dependent variable on the measure of the dependent variable.

A separate Information Theoretic model was developed for each of the three metrics of sea trout population size and rate of change used as response variables. Sea trout catch as a response variable was modelled as a negative binomial distribution, the population rate of change in abundance and sea trout population proportional abundance were modelled as gaussian distributions. Model assumptions were checked by evaluating the regression of modelled and measured values of the dependent variable for all three metrics of populations, as well as by testing for overdispersion.

3.2.2.3 Two-step modelling process

Once the modelling process was established, it was used to answer two questions.

(1) Is the presence or absence of net-pen salmon aquaculture within 30 km of a District acting as a predictor of sea trout populations on the west coast of Scotland?

To answer this question, each measure of abundance was analysed using a subset of data made up of west coast Districts (N=47). Both river specific and climatic environmental variables were selected as outlined in Steps 1 and 2 above for this dataset. In addition to these variables, the categorical Presence/Absence binomial was included at Step 3 as an explanatory variable in the global model.

(2) When net-pen salmon aquaculture is present, is the cumulative biomass within 30 km acting as a predictor of sea trout populations?

To test for a quantitative net-pen biomass effect, a further subset of data comprised of only Districts that had an active net-pen facility within 30 km (Table 3.1) was generated and used in the analysis of each measure of abundance (N=33). River specific and climatic variables were chosen using the analysis outlined in Steps 1 and 2 before all important explanatory variables were added into a global model. A net-pen biomass variable representing the total maximum annual biomass from net-pens occurring within 30 km of the District was also included in the global model (Step 3).

Ecologically relevant interactions were included in the global models. These included specified environmental variable as well as additional aquaculture interactions of ecological interest.

All statistical analysis from this study was conducted in R version 3.6.0 (R Core Team, 2019) using packages MuMIn (Barton, 2019), ggplot (Wickham, 2016), MASS (Venables & Ripley, 2002) and plyr (Wickham, 2011).

3.3 Results

3.3.1 Influence of the Presence of a Net-Pen Salmon Aquaculture Facility

3.3.1.1 Sea trout catch

Sea trout catch across the west coast of Scotland was predicted by several important environmental and climatic variables in addition to the presence or absence of net-pens (Tables A2.2 & A2.3).

Only one final averaged model predicting sea trout catch resulted from the model dredging process at this stage (Step 4) of the analysis. This indicated that all of the variables that were included in the global model (Step 3, see Methods) were highly important and thus included in the final averaged model (Step 4, Table A2.3). This means that all variables are assigned an Importance Value of 1.00 because of their presence in the only averaged model produced.

Sea trout catch was significantly predicted by an interaction between the presence of net-pens and the second order polynomial term of sea temperature ($P < 0.001$) (Table A2.3). Thus, for rivers where net-pens were not present, the predicted sea trout catch increased with sea temperature continuously from ~10.0°C up to ~12°C at which point there was a slight decline (Fig 3.4). However, for rivers where net-pens were present, sea trout catch initially declined as sea temperature rose, but then increased slightly once temperatures reached 11.5°C.

Modelling also showed an important interaction between river length and the presence or absence of net-pens and their effects on sea trout catch ($P < 0.001$) (Table A2.3). Sea trout catch was greater in rivers of longer length but this effect changed depending upon the presence or absence of a net-pen. Rivers without net-pens within 30 km had significantly higher sea trout catches than similarly sized catchments with net-pens present within 30 km (Fig 3.5). As river length declined, the effect strength of the interaction decreased.

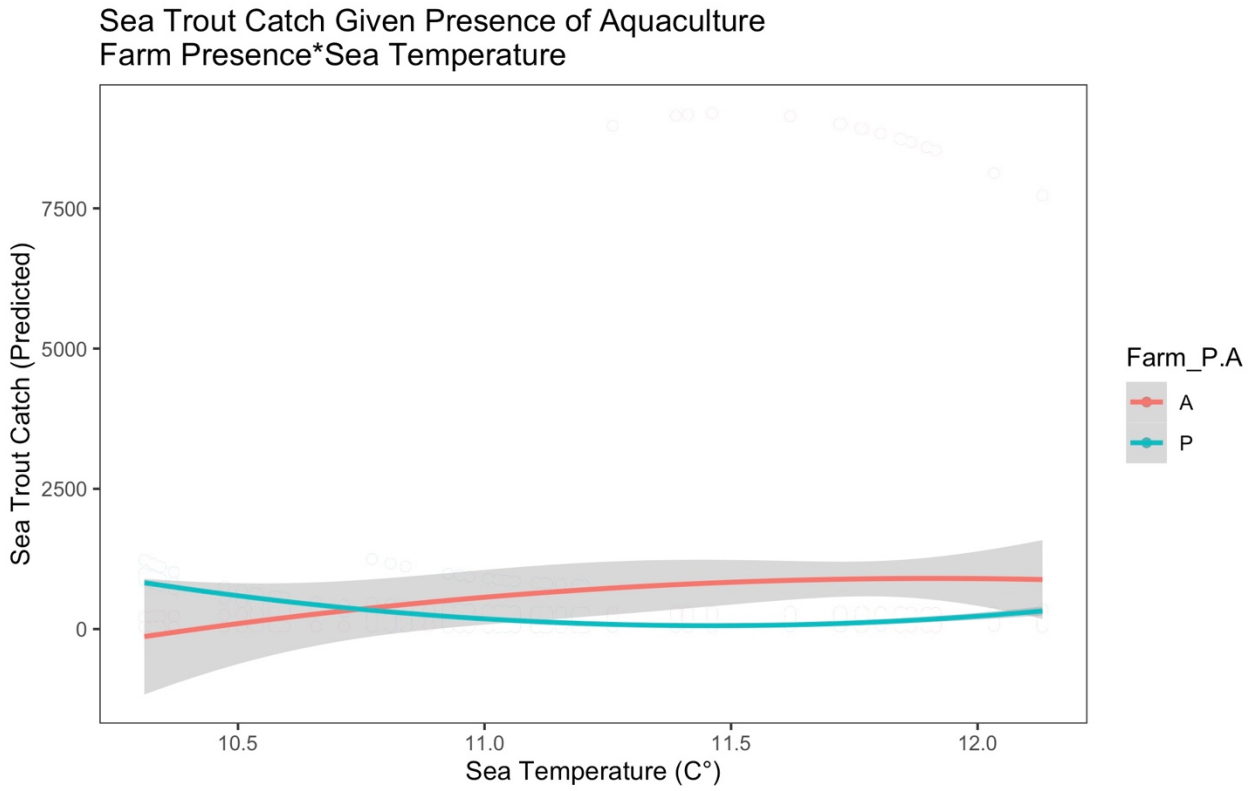


Figure 3.4. The effects of a significant interaction between annual mean sea temperature (C°) and the presence or absence of Atlantic salmon aquaculture facilities within a 30km radius on predicted sea trout catch from 2002 to 2018. Represents the predicted sea trout catch and standard error reported from areas with aquaculture present. Represents the predicted sea trout catch and stardard error reported from areas with aquaculture absent.

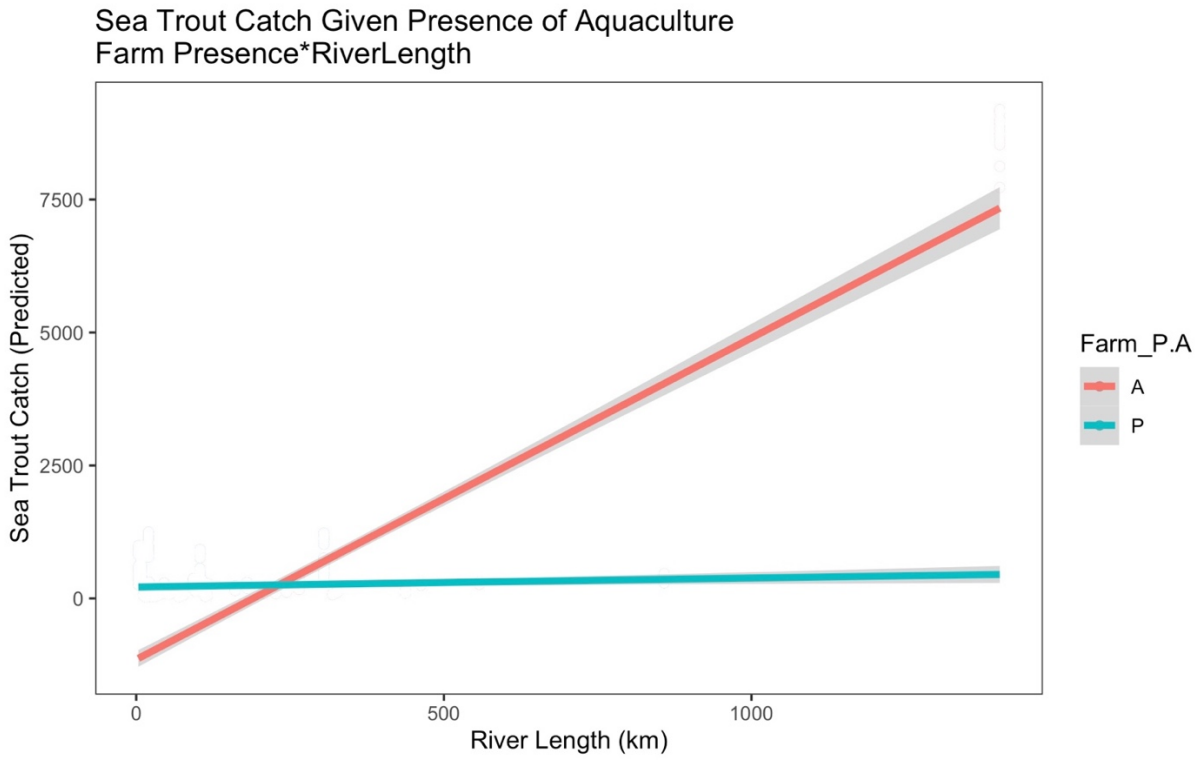


Figure 3.5. The effects of a significant interaction between river length (km) and the presence or absence of Atlantic salmon aquaculture facilities within a 30km radius on predicted sea trout catch from 2002 to 2018. Represents the predicted sea trout catch and standard error reported from areas with aquaculture present. Represents the predicted sea trout catch and stardard error reported from areas with aquaculture absent.

Thus, the positive effect of river length on predicted sea trout catch was reduced in areas with aquaculture facilities present.

Several river specific variables were also shown to be important predictors of sea trout catch after other variables were accounted for. The maximum altitude of a river's catchment was significantly negatively correlated to sea trout catch (P-value <0.001) (Table A2.3). Thus, as the maximum altitude of a river increased, sea trout catch decreased.

The percentage of calcareous geology within a river catchment was significantly negatively correlated to sea trout catch (P-value <0.001) (Table A2.3). Thus, as the percentage of calcareous geology increased, sea trout catch decreased.

The mean river gradient of a catchment was significantly positively correlated to sea trout catch (P-value <0.001) (Table A2.3). Thus, as mean river gradient increased, sea trout catch increased.

The percentage of peatland in a river catchment was significantly positively correlated to sea trout catch (P-value <0.001) (Table A2.3). Thus, as peatland dominance increased, sea trout catch increased.

The percentage of the catchment within a 1:10 year predictive flood area was significantly positively correlated to sea trout catch (P-value <0.001) (Table A2.3). Thus, as the percentage of a catchment within a 1:10 year predictive flooding area increased, sea trout catch increased.

The percentage of solid geology in a river catchment was significantly negative correlated to sea trout catch (P <0.001) (Table A2.3). Thus, as the percentage of solid geology within a catchment increased, sea trout catch declined.

3.3.1.2 Proportional abundance

The proportional abundance of sea trout across the west coast of Scotland was found to be influenced by several important environmental and climatic variables in addition to the presence or absence of aquaculture facilities (Table A2.3).

Modelling showed an important interaction between the presence of net-pens and the second order polynomial term of sea temperature on the proportional abundance of sea trout ($P < 0.001$) (Table A2.3). In areas where net-pens were not present, the predicted proportional abundance of sea trout increased as sea temperature increased continuously from ~10.0°C until temperatures reached ~12°C at which point there was a slight decline (Fig 3.6). However, in areas where net-pens were present, proportional abundance initially declined as sea temperature rose, but then increased slightly when temperatures reached 11.5°C. The Importance Value assigned to this model term by the model dredging process was 1.00, indicating that this interaction was highly important.

An important interaction between river length and the presence or absence of net-pens predicted the proportional abundance of sea trout ($P < 0.001$) (Table A2.3). Proportional abundance was, in general, greater for longer river lengths but this effect was modified depending upon the presence or absence of a net-pen. Rivers in areas without net-pens had a significantly higher proportional abundance than rivers of a similar length that did have net-pens within 30 km (Fig 3.7). As river length declined, the relative difference between the two groups decreased. Thus, the positive effect of river length on predicted proportional abundance was reduced in areas with net-pens present. The Importance Value assigned to this model term by the model dredging process was 1.00, indicating that this interaction was highly important.

Modelling showed an important interaction between winter rainfall and the presence or absence of net-pens. Thus the effect of winter rainfall on the proportional abundance of sea trout depended upon the presence or absence of a net-pen (Table A2.3). This difference in proportional abundance was greater at times of high and low winter rainfall values (Fig 3.8). Districts with net-pens present within 30 km predicted the highest proportional abundances at times of highest rainfall. Districts with no net-pens within 30 km predicted the highest proportional abundance during times of low rainfall. Thus, the positive effect of high levels of winter rain on predicted proportional abundance was enhanced in areas with net-pens present. Although this interaction was not itself statistically significant, the Importance Value assigned to this model term by the model dredging process was 0.87, indicating that this interaction was highly important.

There was an important interaction between river length and mean summer rainfall. There was a significant negative relationship between proportional abundance and summer rainfall ($P=0.005$) (Table A2.3). Predicted proportional abundance always increased with

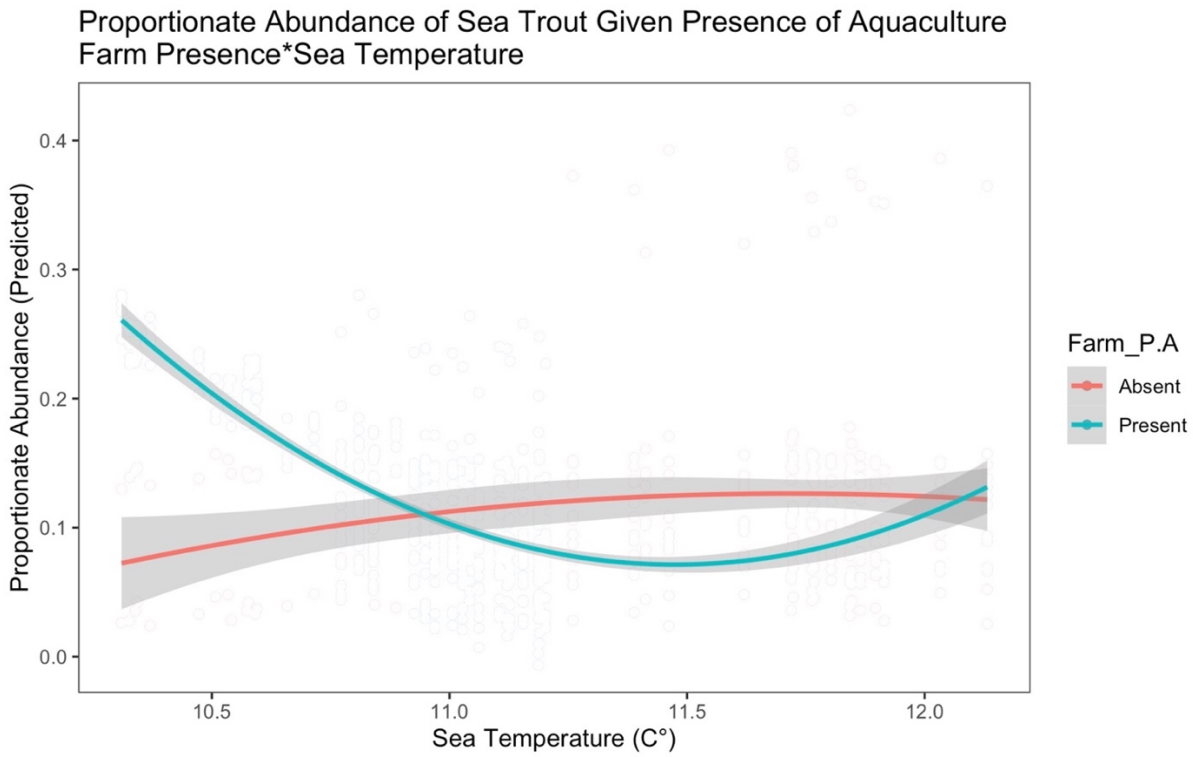


Figure 3.6. The effects of a significant interaction between annual mean sea temperature (C°) and the presence or absence of Atlantic salmon aquaculture facilities within a 30km radius on predicted proportionate abundance of sea trout from 2002 to 2018. Represents the predicted proportionate abundance and standard error reported from areas with aquaculture present. Represents the predicted proportionate abundance and standard error reported from areas with aquaculture absent.

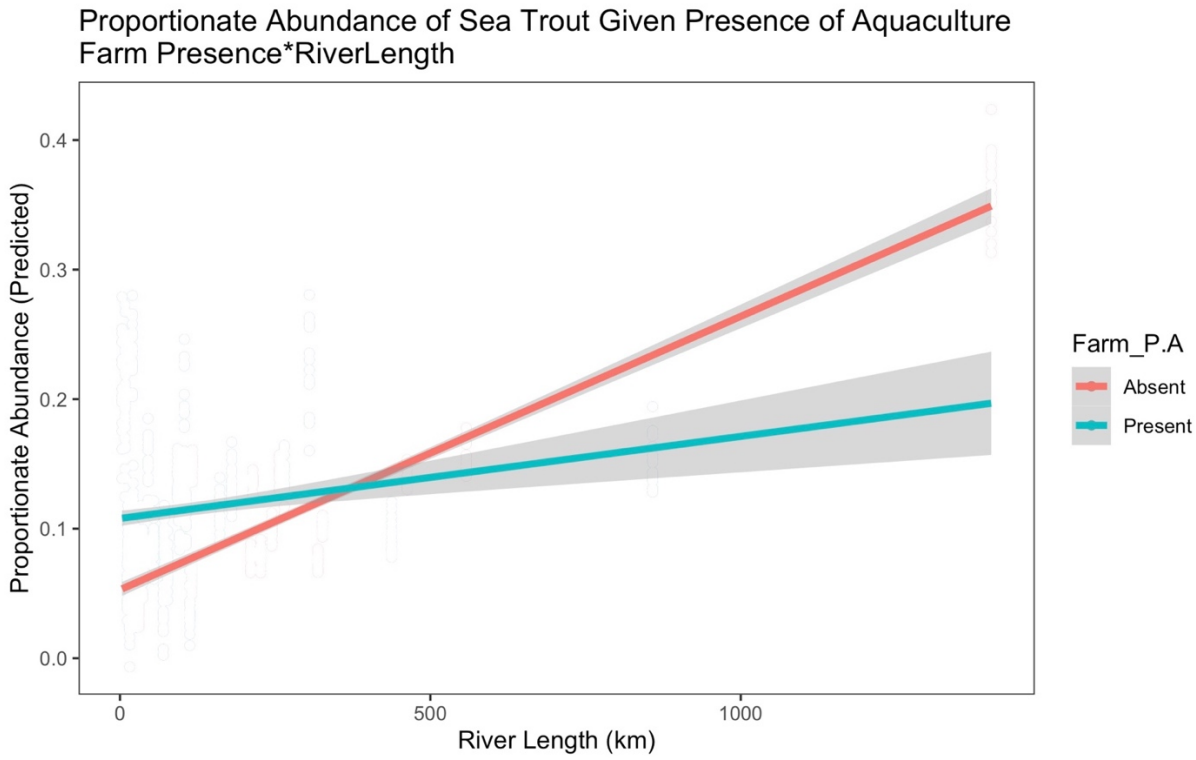


Figure 3.7. The linear relationship of a significant interaction between river length (km) and the presence or absence of Atlantic salmon aquaculture facilities within a 30km radius on predicted proportionate abundance of sea trout from 2002 to 2018. Represents the predicted proportionate abundance and standard error reported from areas with aquaculture present. Represents the predicted proportionate abundance and standard error reported from areas with aquaculture absent.

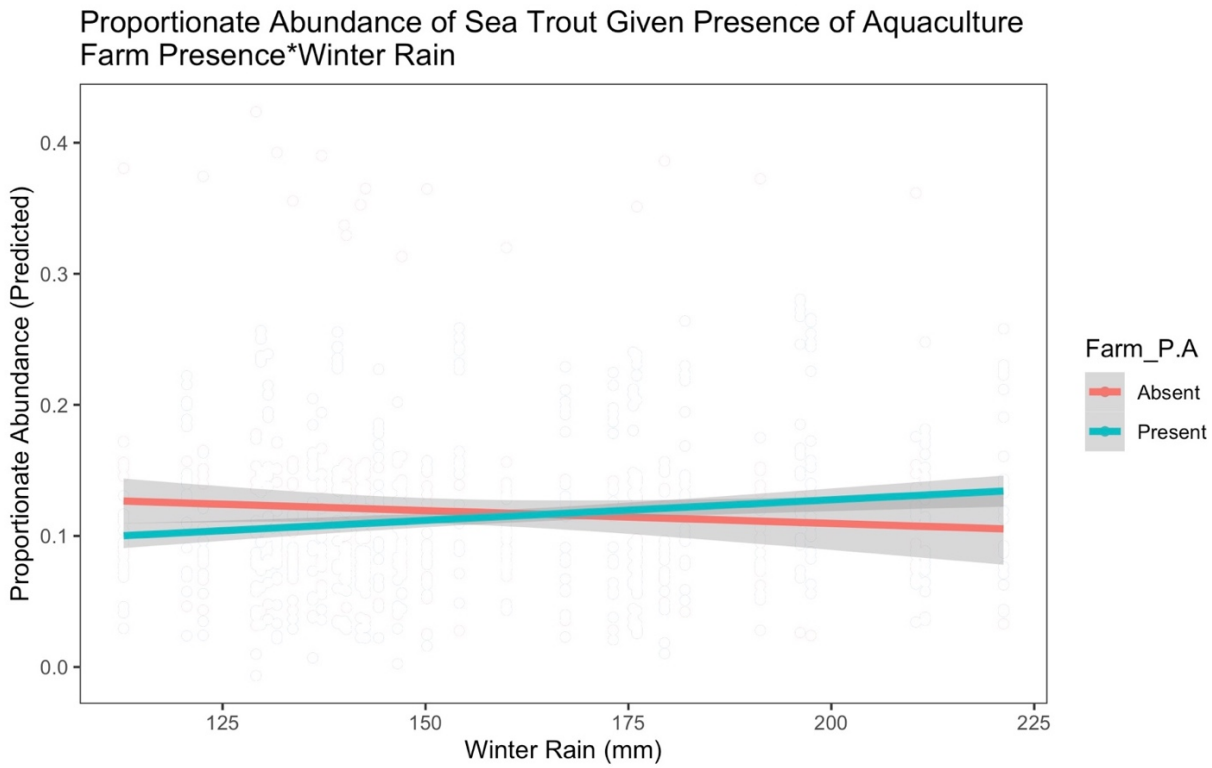


Figure 3.8. The linear relationship of an important interaction between mean monthly winter rainfall (mm) and the presence or absence of Atlantic salmon aquaculture facilities within a 30km radius on predicted proportionate abundance of sea trout from 2002 to 2018. Represents the predicted proportionate abundance and standard error reported from areas with aquaculture present. Represents the predicted proportionate abundance and stardard error reported from areas with aquaculture absent.

increasing river length, regardless of rainfall, however Districts with shorter river lengths reported an increasing proportional abundance as summer rainfall increased, while Districts with longer river lengths reported a decreasing proportional abundance as summer rainfall increased. The Importance Value assigned to this model term by the model dredging process was 1.00, indicating that this interaction was highly important.

An important interaction between the mean river gradient of a catchment and mean winter rainfall also emerged from the modelling. There was a negative relationship between proportional abundance and winter rainfall (Table A2.3). Predicted proportional abundance always decreased with increasing gradient, regardless of rainfall, however catchments with a lower mean river gradient reported a higher proportional abundance of sea trout when mean monthly winter rainfall was elevated than when rainfall was low. In catchments with a higher mean river gradient, higher predicted proportional abundance was reported when winter rainfall was low and decreased as rainfall increased. Thus, the negative effect of river gradient on proportional abundance was enhanced by the effect of winter rainfall during this time period. Although this interaction was not statistically significant, the Importance Value assigned to this model term by the model dredging process was 0.87, indicating that this interaction was highly important.

Several river specific variables were also important potential drivers of proportional abundance after other variables were accounted for. The percentage of calcareous geology within a catchment ($P < 0.001$) (Table A2.3) was significantly negatively correlated to proportional abundance. Thus, as the percentage of calcareous geology increased, the proportional abundance of sea trout decreased. The Importance Value assigned to this model term by the model dredging process was 1.00, indicating that this variable was highly important.

The maximum altitude of a river ($P < 0.001$) (Table A2.3) was significantly negatively correlated to proportional abundance. Thus, as the maximum altitude of a catchment increased, the proportional abundance of sea trout decreased. The Importance Value assigned to this term by the model dredging process was 1.00, indicating that this variable was highly important.

The percentage of peatland within a catchment significantly positively predicted the proportional abundance of sea trout ($P < 0.001$) (Table A2.3). Thus, as peatland dominance increased, the proportional abundance of sea trout also increased. The Importance Value

assigned to this term by the model dredging process was 1.00, indicating that this variable was highly important.

The percentage of solid geology within a District's catchment was significantly negative correlated to the proportional abundance of sea trout (P <0.001) (Table A2.3). Thus, as the percentage of solid geology within a catchment increased, proportional abundance declined. The Importance Value assigned to this term by the model dredging process was 1.00, indicating that this variable was highly important.

The percentage of the catchment within a 1:10 year predictive flood area was significantly positively correlated to the proportional abundance of sea trout (P-value <0.001) (Table A2.3). Thus, as the percentage of a catchment within a 1:10 year predictive flooding area increased, proportional abundance increased. The Importance Value assigned to this term by the model dredging process was 1.00, indicating that this variable was highly important.

3.3.2 Predictors of Sea Trout Population Size in the Presence of Net-Pen Aquaculture

3.3.2.1 Sea trout catch

In Districts with active net-pens within 30 km, sea trout catch was predicted by several variables (Tables A2.4 & A2.5).

An important interaction between the net-pen biomass and the polynomial term of sea temperature as an effect on sea trout catch was identified. Thus there was a significant relationship between predicted sea trout catch and sea temperature but the effect of this relationship varied with the biomass of salmon in net-pens (P = 0.004) (Fig 3.9 & Table A2.5). To visually represent the interaction between these two predicting variables and its effect on sea trout catch, sea temperature data were discretised into three levels (Low= 10.0°C-10.75°; Medium= 10.76°-11.50°C; High= 11.51°C-12.25°C) and regression lines at each of these levels were plotted using the predicted values produced by the model. The resulting plot (Fig 3.9) demonstrated how sea trout catch responded to net-pen biomass at different temperature levels.

At low temperatures, sea trout catch increased with net-pen biomass, while in areas of high temperatures, sea trout catch decreased as net-pen biomass increased. The Importance

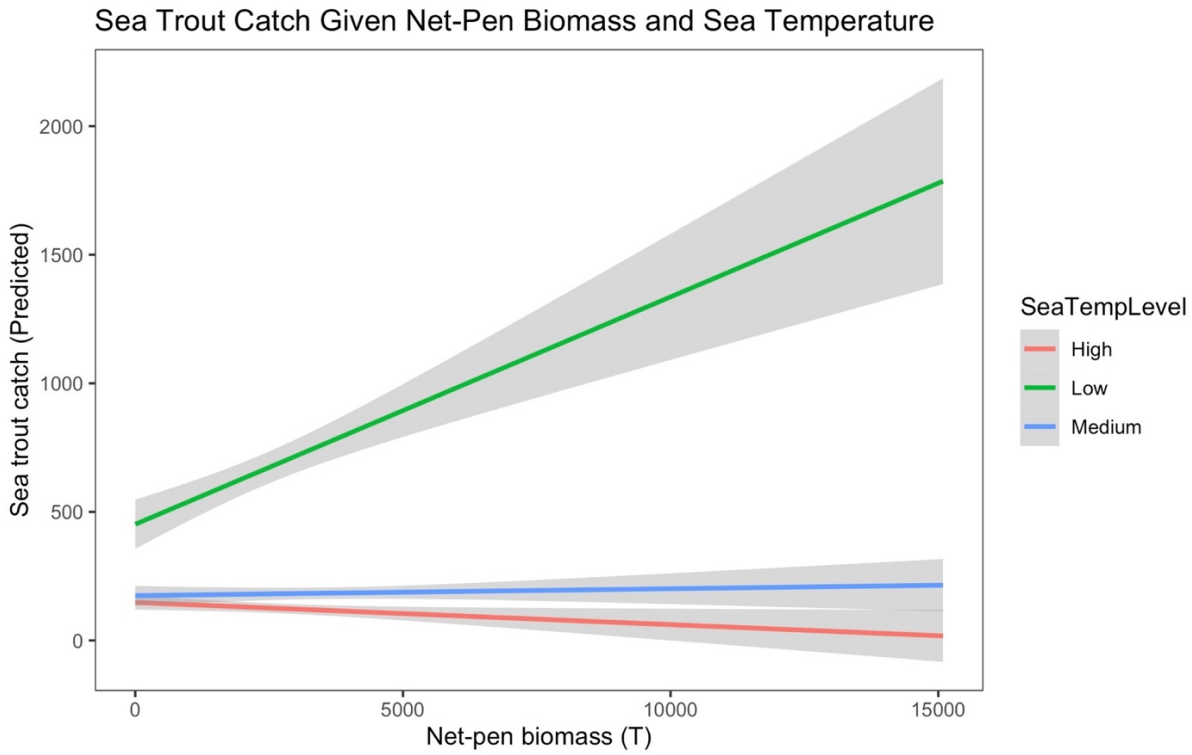


Figure 3.9 The significant interaction between net-pen biomass (T) and sea temperature (C°) and their effect on predicted sea trout catch. Sea temperature levels are Low= 10.0°C-10.75°; Medium= 10.76°-11.50°C; High= 11.51°C-12.25°C. ( ), ( ) and ( ) represent the linear regressions and standard errors between predicted sea trout catch and net-pen biomass at low, medium and high annual sea temperatures, respectively.

Value assigned to this model term by the model dredging process was 1.00, indicating that this interaction was highly important.

Modelling showed that an important interaction between the net-pen biomass and mean monthly winter rainfall had an effect on predicted sea trout catch (P = 0.005) (Fig 3.10 & Table A2.5). To visually represent the interaction between these three variables, winter rainfall data were discretised into three levels (Low= 110-150 mm; Medium= 151-190 mm; High= 190-225 mm) and regression lines at each of these levels were plotted using the predicted values produced by the model. The resulting plot demonstrates how sea trout catch responded to net-pen biomass at different winter rainfall levels.

In periods of low winter rainfall, predicted sea trout catches decreased as net-pen biomass increased. In periods of high and medium winter rainfall, sea trout catches increased with increasing net-pen biomass. The Importance Value assigned to this model term by the model dredging process was 1.00, indicating that this interaction was highly important.

The percentage of solid geology within a river catchment was typified by a significant negative relationship with sea trout catch from 2002- 2018 (P <0.001) (Table A2.5), indicating that as the percentage of solid geology increased, sea trout catch declined. The Importance Value assigned to this model term by the model dredging process was 1.00.

The percentage of calcareous geology within a river catchment was typified by a significant negative relationship with sea trout catch from 2002- 2018 (P <0.001) (Table A2.5), indicating that as the percentage of calcareous geology increased, sea trout catch declined. The Importance Value assigned to this model term by the model dredging process was 1.00.

The maximum altitude of a river catchment was typified by a significant negative relationship with sea trout catch from 2002- 2018 (P = 0.016) (Table A2.5), indicating that as maximum altitude increased, sea trout catch declined. The Importance Value assigned to this model term by the model dredging process was 1.00.

The total river length within a District's catchment area was typified by a positive relationship with sea trout catch from 2002- 2018 (P = 0.001) (Table A2.5), indicating that as river length increased, sea trout catch also increased. The Importance Value assigned to this model term by the model dredging process was 1.00.

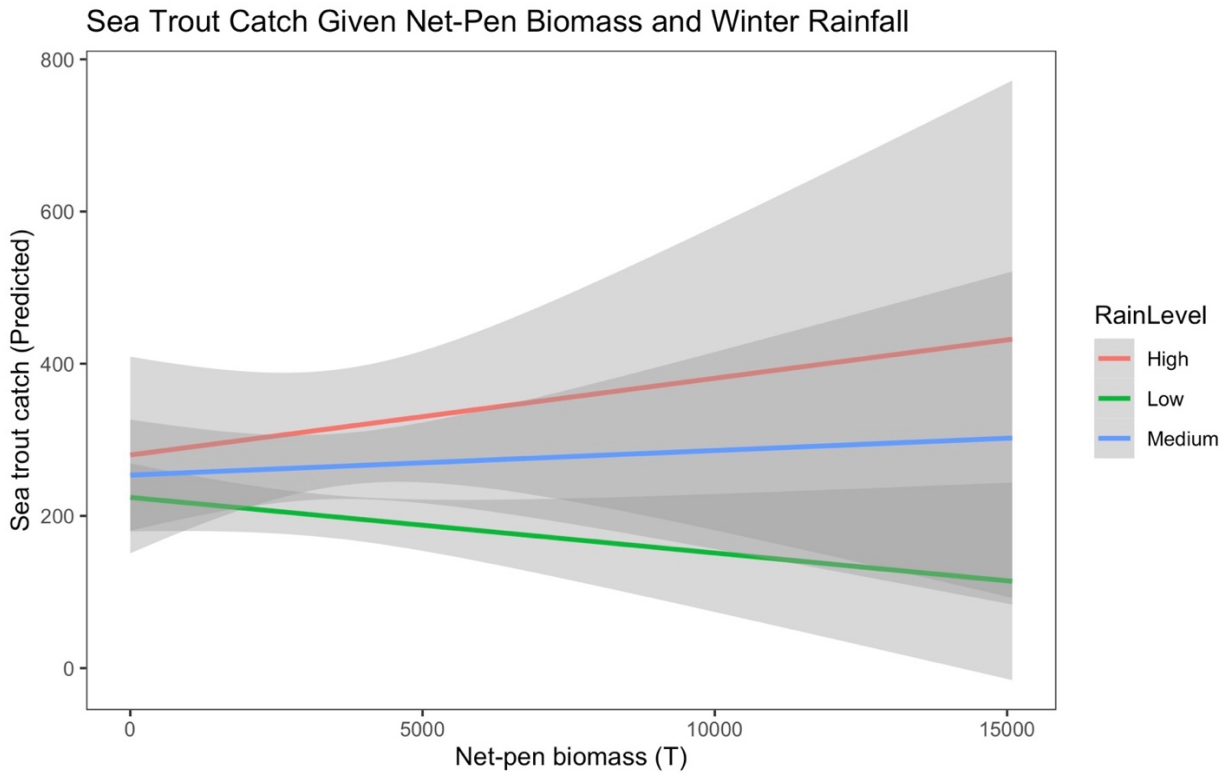


Figure 3.10 The significant interaction between net-pen biomass (T) and mean monthly winter rainfall (mm) and their effect on predicted sea trout catch. Winter rainfall levels are Low= 110-150mm; Medium= 151-190mm; High= 190-225mm. ( ), ( ) and ( ) represent the linear regressions and standard errors between predicted sea trout catch and net-pen biomass at low, medium and high mean month winter rainfall, respectively.

The percentage of peatland within a District's catchment area was typified by a positive relationship with sea trout catch from 2002- 2018 (P =<0.001) (Table A2.5), indicating that as peatland dominance increased, sea trout catch also increased. The Importance Value assigned to this model term by the model dredging process was 1.00.

Mean summer rainfall levels were typified by a significant positive relationship with sea trout catch from 2002- 2018 (P = 0.017) (Table A2.5), indicating that as summer rainfall increased, sea trout catch also increased. The Importance Value assigned to this model term by the model dredging process was 1.00.

The percentage of the catchment within a 1:10 year predictive flood area was significantly positively correlated sea trout catch (P-value <0.001) (Table A2.5). Thus, as the percentage of a catchment within a 1:10 year predictive flooding area increased, sea trout catch increased. The Importance Value assigned to this term by the model dredging process was 1.00, indicating that this variable was highly important.

Mean summer NAO values were typified by a negative relationship with sea trout catch from 2002- 2018 (P = 0.192) (Table A2.5), indicating that as summer NAO increased, sea trout catch declined. Although this relationship was not significant, the Importance Value assigned to this model term by the model dredging process was 0.80 indicating that it was highly important.

3.3.2.2 Proportional abundance

Only one final averaged model resulted from the model dredging process at this stage of the proportional abundance analysis (Step 4). This indicated that all of the variables that were included in the global model (Step 3, see Methods) were considered highly important and were included in the final averaged model (Step 4, Table A2.5). This means that all variables are assigned an Importance Value of 1.00 because of their presence in the only averaged model produced.

For areas where net-pens are within 30 km of the main river mouth, proportional abundance of sea trout was influenced by several different variables (Table A2.5).

There was an important interaction between the net-pen biomass and river length in predicting sea trout proportional abundance. Thus there was a significant negative relationship between proportional abundance of sea trout and river length which was modified by net-pen biomass (P = 0.024) (Fig 3.11 & Table A2.5). To visually represent the interaction between these two variables and their effect on proportional abundance of sea trout, river length was discretised into two levels (Short= 0-500 km; Long= 500-1,000 km) and regression lines at both of these levels were plotted using the predicted values produced by the model. The resulting plot demonstrates how the proportional abundance of sea trout responded to net-pen biomass relative to river length.

The predicted proportional abundance of a river declines as biomass increases, regardless of river length. However, longer rivers experienced a considerably greater decline in proportional abundance than shorter rivers (Fig 3.11).

There was an important and significant relationship between proportional abundance of sea trout and sea temperature (P <0.001) but that effect was dependent upon net-pen biomass (Fig 3.12 & Table A2.5). To visually represent the interaction between these three variables, sea temperature was discretised into three levels (Low= 10.0°C-10.75°C; Medium= 10.76°-11.50°C; High= 11.51°C-12.25°C) and regression lines at each of these levels were plotted using the predicted values produced by the model. The resulting plot demonstrates how the proportional abundance of sea trout responded to net-pen biomass at different temperature levels.

At low sea temperatures there was a positive predicted effect of net-pen biomass on the proportional abundance of sea trout. At medium and high sea temperatures, however, this effect was reversed, indicating a decline in the proportional abundance of sea trout with increasing net-pen biomass (Fig 3.12).

The percentage of calcareous geology within the catchment area was significantly negatively correlated with proportional abundance (P <0.001) (Table A2.5). Thus, as the percentage of calcareous geology increased, the predicted proportional abundance of sea trout decreased.

The percentage of solid geology within the catchment (P < 0.001) was significantly negatively correlated with predicted proportional abundance (Table A2.5). Thus, as the

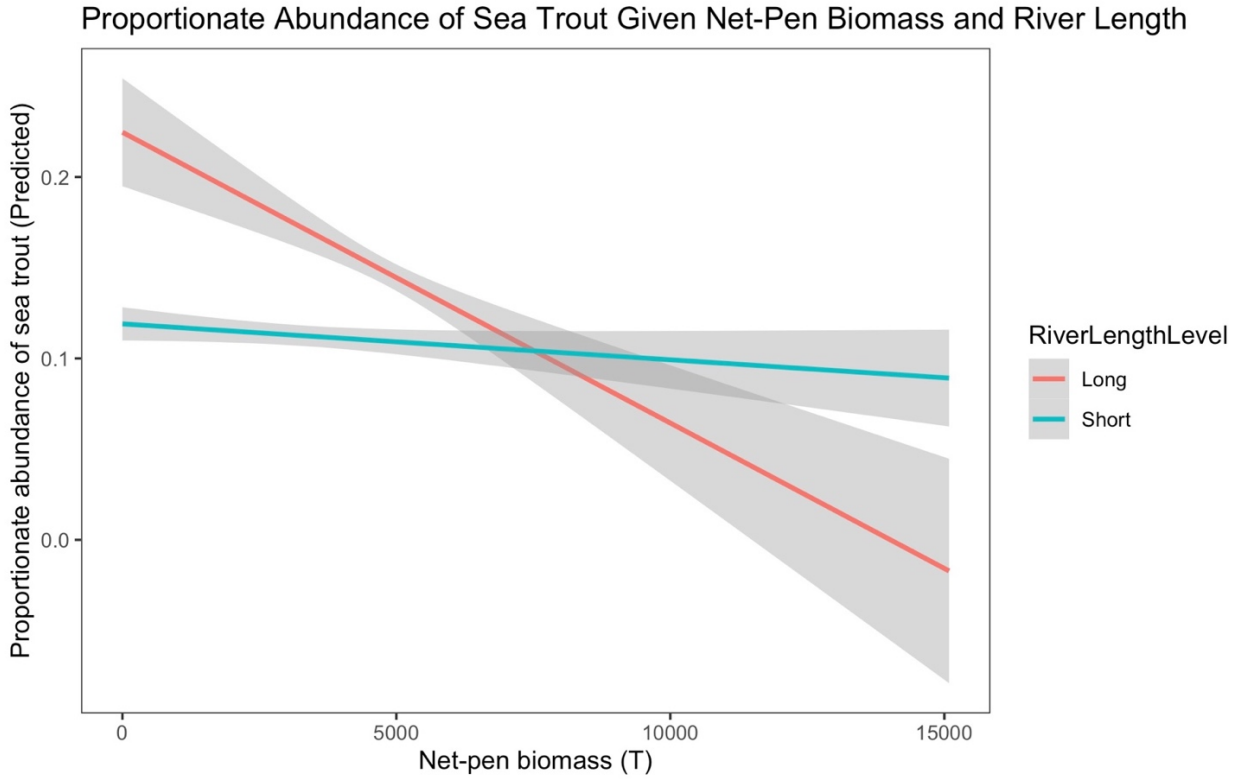


Figure 3.11 The significantly different relationships between net-pen biomass (T) and predicted proportionate abundance of sea trout given river length (km). River length levels are Short= 0 - 500km; Long = 0 - 1000km. (—) and (—) represent the linear regressions and standard errors between predicted proportionate abundance and net-pen biomass at long and short river lengths, respectively.

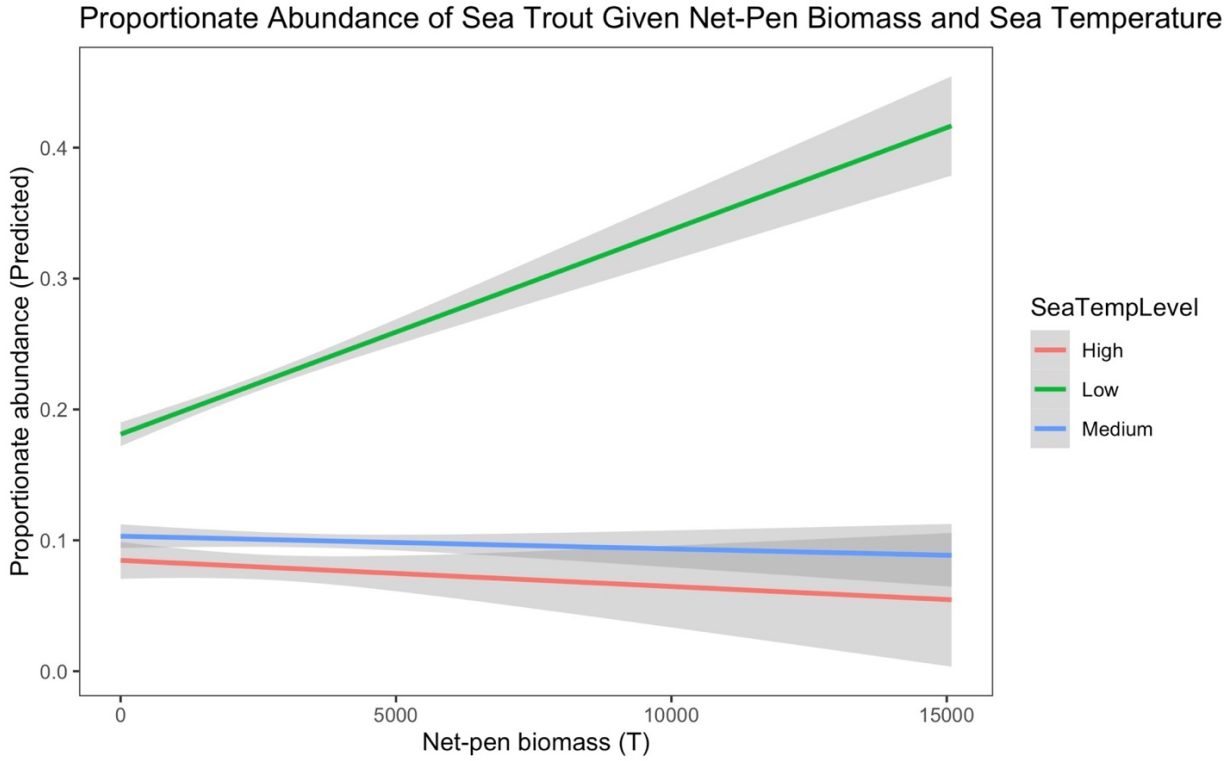


Figure 3.12 The significantly different relationships between net-pen biomass (T) and predicted proportionate abundance of sea trout at different sea temperature ranges (°C). Sea temperature levels are Low= 10.0°C-10.75°C; Medium= 10.76°-11.50°C; High= 11.51°C-12.25°C. ( ), ( ) and ( ) represent the linear regressions and standard errors between predicted proportionate abundance of sea trout and net-pen biomass at low, medium and high mean annual sea temperatures, respectively.

percentage of solid geology within a catchment increased, proportional abundance of sea trout decreased.

The maximum altitude in a river catchment was significantly negatively correlated with proportional abundance (P = 0.029) (Table A2.5). Thus, as the maximum altitude of a river increased, predicted proportional abundance of sea trout decreased.

The second order polynomial term of mean summer NAO values was significantly negatively correlated with predicted proportional abundance (P = 0.005) (Table A2.5). Thus, as the summer NAO values increased, proportional abundance of sea trout decreased.

The percentage of peatland was significantly positively correlated (P <0.001) with proportional abundance (Table A2.5). Thus, as peatland dominance increased, the predicted proportional abundance of sea trout also increased.

The percentage of the catchment within a 1:10 year predictive flood area was significantly positively correlated the proportional abundance of sea trout (P-value <0.001) (Table A2.5). Thus, as the percentage of a catchment within a 1:10 year predictive flooding area increased, predicted proportional abundance increased.

3.3.3 Rate of Change

There were no significant drivers of rate of change.

3.4 Discussion

In this study we make use of a long term dataset comprising annual rod and line catches of sea trout, from 47 populations, broadly covering a geographic area that also supports net-pen salmon aquaculture in Scotland. Rod catches of salmonids have been shown to be a valuable measure of population size (Davidson *et al*., 2017; Smith *et al*., 2000 Crozier & Kennedy, 2001; Youngson *et al*., 2002; Thorley *et al*., 2005; Beaumont *et al*., 1991) and have widely been used as such (see for example: Harris & Evans, 2017; Höjesjö al., 2017; Davidson *et al*., 2017).

This study addresses two specific hypotheses.

3.4.1 Hypothesis 1:

(1) The presence of net-pen salmon aquaculture influences the population size of sea trout.

It is clear from the study presented here and in a related study (Moore *et al*. in prep; Chapter 2) that sea trout populations in Scotland are affected by a range of instream, geographic and climatic variables that influence population size. Here we provide evidence that the presence of net-pen Atlantic salmon aquaculture facilities within 30 km of the mouth of a river supporting sea trout also has had an effect on the size of the sea trout population in that river. However, we also show that this effect is often complex in nature and works in combination with other variables.

The polynomial term of annual mean sea temperature was an important negative predictor of population size, while the presence and absence of net-pen salmon aquaculture were important positive predictors of population size. However, there was also an important interaction between these two, suggesting a complex interrelationship between them after other variables were accounted for.

In general, when annual mean sea temperatures increased over the range over the years examined in this study, modelling showed an increasing negative effect of net-pen presence on both sea trout catch and proportional abundance of sea trout. At low sea temperatures (below ca 10.8°C), the presence of aquaculture net-pens had a positive effect on sea trout population size (Figs 3.4 & 3.6).

This relationship could be the result of several factors, one of which involves the natural life cycle of salmon lice. The development rates of salmon lice populations have been shown to increase as sea temperatures increase up to 21°C (Tucker *et al*., 2000; Hamre *et al*., 2019). Therefore, one possibility for this observed effect is that salmon lice populations are increasing during warmer years resulting in higher infection pressure on sea trout populations and ultimately increased mortality. An alternative, but not mutually exclusive, explanation is that increasing sea temperatures may have an impact on marine fish which may have an indirect effect on sea trout through competition or predation interactions (Peck & Pinnegar, 2019). Whatever the mechanism of change, it is likely that climate

change is going to increase the negative effect of net-pen salmon aquaculture on sea trout populations described here.

We also show a second complex effect of the presence of net-pen aquaculture on sea trout populations. A strong driver for sea trout population size was river length. However, there was a statistically important interaction between river length and the presence or absence of net-pen aquaculture, indicating that there was a complicated relationship between them after other variables were accounted for.

Overall, longer rivers produced larger predicted sea trout populations. This effect has also been shown over a longer time period and over a greater geographic range than that presented here (Moore *et al*., in prep.; Ch 2). There are several possible explanations for this; longer rivers are likely to have more habitat available to meet the needs of all the freshwater life stages of sea trout than smaller rivers; larger rivers may also be significantly more resilient to change than smaller rivers. However, this effect varied strongly between areas with aquaculture facilities present or absent, indicating a more complex relationship between the two variables.

In longer rivers, higher sea trout populations were predicted in areas where net-pens were not present. However, for rivers where net-pens were located within 30 km of the river, the positive effect of larger river size was severely eroded. Modelling demonstrated that although there are slightly higher predicted populations in short rivers where net-pens are present, this comprised a small number of the total sea trout populations in this study. Furthermore, the predicted population size of rivers where net-pens are present remain at similar levels even as river length increases, whereas the predicted values of rivers where net-pens are not present increase significantly as river length increases. This mechanism was shown for both sea trout catch and the proportional abundance of sea trout.

Therefore, the effect of longer river length supporting larger sea trout populations, potentially through the provision of a greater variety of habitat types or through greater population resilience, is markedly eroded by the presence of net-pen salmon aquaculture. This points to sea trout populations in rivers adjacent to net-pen salmon aquaculture units being less robust than expected for their habitat type.

There were three additional interactions that were important predictors of the relative sea trout abundance of individuals rivers as a proportion of the 47 rivers included in this dataset.

Mean monthly winter rainfall was not an important predictor of the proportional abundance of a population. However, there was a highly important interaction between winter rainfall and the presence/absence of net-pen aquaculture, indicating a complex interrelationship between them after other variables were accounted for.

In locations where net-pens were absent, winter rainfall had a negative impact on the proportional abundance sea trout populations, indicating that overall heavy winter rainfall depressed abundance. This effect has also been shown over a wider geographic area and a longer time period (Moore *et al*., in prep; Chapter 2) The finding that sea trout populations are declining when winter rainfall increases could be due to a variety of factors. Increased winter rainfall can lead to extreme flooding and ultimately juvenile fish strandings and/or redd washouts which can in turn reduce the number of trout present in any year-class (Jonsson & Jonsson, 2009b). Furthermore, a combination of high river flows (resulting from high winter rainfall), overgrazing and development in riparian zones may lead to the degradation of freshwater habitat as the structural stability of river banks is eroded (Hendry *et al*., 2003). This in turn may inhibit a river's ability to buffer heavy rainfall and can lead to further flooding.

In locations where open-net pens were present, winter rainfall had a positive influence on proportional abundance (Fig 3.8), indicating that heavy winter rainfall led to a slight increase in the proportional abundance of sea tout populations. One explanation for this result could be related to salmon lice infestation levels. Although increased densities are expected during the spring and summer months as temperatures rise, salmon lice can still develop and reproduce in sea temperatures above 4°C (Boxaspen, 2006). Therefore, in areas where net-pens are present, epizootic outbreaks are still possible over the winter.

Salmon lice populations often remain at shallow depths in the water column, although research has demonstrated that lice show diel vertical migration patterns, indicating sensitivity to light, temperature and salinity levels (McKibben & Hay, 2004; Hamre *et al*., 2017). Heutch *et al*. (1995) reported that lice will move between depths of 0 m to 6 m from the surface, preferring shallower depths during the daylight. This vertical distribution

overlaps with the swimming depth preferences of sea trout that range from 0.4 m to 6.4 m (mean depth was 1.7m; Eldøy *et al*., 2017) and could result in the increased likelihood of an individual fish becoming heavily infested with salmon lice in locations with high lice densities, such as areas with net-pens. However, salmon lice have a low tolerance for low salinity levels (Bricknell *et al*., 2006; Rees *et al*., 2015). As salinity levels decline below 30, salmon lice experience limited development, decreased abundance and ultimately mortality during prolonged periods in low salinity areas (Johnson & Albright, 1991; Thorstad *et al*., 2015).

Heavy winter rainfall would increase the amount of freshwater flowing into coastal zones from rivers and thus dilute the surface water in these areas. The decline in salinity, and the resulting brackish conditions, has the potential to reduce the parasite loads on sea trout populations utilizing said coastal zones. Therefore, sea trout populations in areas with open-net pens may benefit from heavy rainfall.

3.4.2 Hypothesis 2:

(2) The annual maximum biomass of net-pen salmon aquaculture units within 30 km of a river supporting sea trout has an influence on the sea trout population size.

Three catchment and climatic variables and their interactions were consistently identified by the Information Theoretic modelling analysis as important predictors of sea trout population size in rivers with net-pens present within 30 km (N=33) given the cumulative annual biomass produced there (hereafter referred to as net-pen biomass).

As described above, a statistically important predictor of sea trout population size was sea temperature, in that as sea temperatures increased, sea trout populations decreased. Additionally, net-pen biomass was also an important predictor, and as net-pen biomass increased, sea trout populations decreased. In the modelling presented here, there was also an important interaction between net-pen biomass and the polynomial term of sea temperature, suggesting a complex interrelationship between them after other variables were accounted for (Figs 3.9 & 3.12).

In areas of low sea temperature (below 10.75°C), sea trout populations showed an increase as net-pen biomass increased. In areas of high sea temperature (above 11.50°C), sea trout populations showed a decline as net-pen biomass increased.

This relationship can be explained by a similar mechanism that is thought to be operating in the interaction between the presence or absence of net-pens and sea temperature. For example, salmon lice populations are known to increase their development speed in warmer temperatures, therefore as sea temperature increases, it is feasible that salmon lice populations may increase, therefore causing a greater negative impact on local sea trout populations (Boxaspen, 2006; Hamre *et al*., 2019). But in areas with cool sea temperatures, salmon lice populations are not able to increase as quickly (Costello, 2006), and therefore salmon lice impacts on trout populations remain relatively lower.

A strong driver of the proportional abundance of sea trout was river length. Predicted proportional abundance increased as river length increased. Net-pen biomass was also an important predictor of proportional abundance, and as net-pen biomass increased, predicted proportional abundance declined. However, there was an important interaction between river length and net-pen biomass, indicating that there was a relationship between them after other variables were accounted for (Fig 3.11).

The predicted proportional abundance of sea trout decreased across all rivers as net-pen biomass increased, however, longer rivers reported a greater decline in their proportional abundance than shorter rivers.

This result demonstrates that all rivers show a decline in their sea trout populations as net-pen biomass increases, a similar finding has been shown in other studies that have documented declines in salmonid populations in areas of intensive aquaculture (Thorstad & Finstad, 2018).

Mean monthly winter rainfall was important positive predictor of sea trout population size, but on its own was not a statistically significant effect (Table A2.5). Net-pen biomass was also an important and significant predictor of sea trout population size. As net-pen biomass increased, sea trout biomass decreased. However, there was an important interaction between these two variables, indicating that there was a more complex interrelationship between them after other variables were accounted for.

The negative effects of increasing net-pen biomass on the sea trout population were greater during years of low winter rainfall (Fig 3.10). As rainfall increased, the effects of increasing net-pen biomass lessened and sea trout populations increased slightly.

This relationship can be explained by a similar mechanism that is thought to be operating in the interactions between the presence or absence of aquaculture and winter rain, i.e. an increase in winter rainfall could help manage the densities of salmon lice on sea trout by decreasing the salinity in coastal zones where sea trout are thought to spent a large amount of time (Bricknell *et al*., 2006; Rees *et al*., 2015).

3.4.3 Other Important Predictors

Several other environmental variables that relate directly to the catchment of origin of the local sea trout population were frequently identified as important predictors of sea trout populations in the both the presence/absence models and the net-pen biomass models. Thus, the percentages of solid geology and calcareous geology within a catchment (both negatively), percentage of peatland (positively), river gradient (positively), maximum river altitude (negatively) and the percentage of the catchment within a 1:10 year predictive flood area (positively) all have an effect on the sea trout population size. These features are largely fixed attributes of the catchment and mostly invariant over long time periods. A brief explanation about the individual relationships between these predictors and sea trout populations can be found in Table 3.2. The relationships between these environmental parameters and sea trout populations are summarised in more detail in Chapter 2 (Moore *et al*., in prep).

3.4.4 Broad Themes

This study has demonstrated that 1) sea trout populations are reacting differently in areas with and without net-pen salmon aquaculture, 2) there is a negative effect of increasing net-pen biomass on sea trout populations in areas where is net-pen salmon aquaculture is present within 30 km and 3) this relationship is often complex and is dependent upon characteristics of the catchment supporting the local sea trout population and at times upon broad scale climatic conditions. There are now numerous studies that have implicated the increase in net-pen salmon aquaculture as one of the driving forces behind the decline of salmonid populations. The mechanism frequently identified is an increase in salmon lice densities, leading to the premature entry of anadromous sea trout into freshwater resulting

Table 3.2. Summary table of important environmental predictors of sea trout populations as determined during the model dredging process. "Reasoning behind relationship" column provides a brief explanation of the relationship between the variables and sea trout populations. Further information about these relationships can be found in Chapter 2 (Moore et al., in prep).

Variable	Effect	Reasoning behind relationship	References
Mean river graident	Positive	Rivers with higher mean gradients are found primarily in the north-west of Scotland or on the islands. These habitats are known for supporting trout populations, but not many other species	Frost & Brown (1967); Campbell (1971)
Mean river graident and winter rainfall	Negative	There could be an elevated spate effect of high rainfall on high gradient rivers where water velocity and discharge is inevitably higher in steep gradients resulting in redd washout or direct physical effects on overwintering sea trout fry or parr (Jonsson & Jonsson, 2009).	Jonsson & Jonsson (2009b)
Summer rainfall	Positive	High rainfall in summer provides more varied habitat for different life stages of trout that are in freshwater, helps to keep water temperatures cool, could help control salmon lice populations in coastal areas by decreasing salinity levels	Jonsson & Jonsson (2011)
Summer rainfall and river length	Negative	Longer rivers reported declines in sea trout populations as rain increased while shorter rivers reported increases in sea trout populations. Speculatively, during periods of extreme high flows, catching fish becomes more difficult resulting in lower population numbers. In shorter rivers, increased rainfall could result in additional habitat becoming available to support more juveniles	
Percentage of solid geology	Negative	High levels of solid geology substrate provide poor invertebrate habitat and little cover from elevated temperatures or predators	Palm *et al*. (2006); Jonsson & Jonsson (2011)
Peatland dominance	Positive	Catchments with high peatland dominace are often better suited to trout populations more so than salmon or other species, but are also thought to be nutrient poor which could result in high intra-species competition leading to more trout migrating to sea	Frost & Brown (1967); Chapman *et al*. (2012)
Percentage of calcareous geology	Negative	Calcareous based catchments are known to be highly productive and capable of supporting a wide diversity of flora and fauna. Lower sea trout populations could be due to 1) low trout productivity due to high inter-species competion or 2) high level of freshwater-resident trout that chose to remain in productive freshwater habitats	Frost & Brown (1967); Montorio *et al*. (2018).

Table 3.2 (continued). Summary table of important environmental predictors of sea trout populations as determined during the model dredging process. "Reasoning behind relationship" column provides a brief explanation of the relationship between the variables and sea trout populations. Further information about these relationships can be found in Chapter 2 (Moore et al., in prep).

Variable	Effect	Reasoning behind relationship	References
Maximum river altitude	Negative	Trout populations based in catchments in high altitudes are more likely to choose freshwater-resident life hisotry strategies	Bohlin et al. (2001); Prodöhl *et al.* (2019)
1:10 predictive flood area	Positive	Most of the catchments with a high percentage of area within a flood "zone" were located in the north of Scotland. A similar mechanism to that of river gradient, peatland dominance and % of calcareous geology could be working for this predictor in that north Scotland is thought to provide good habitat for *S. trutta*	Frost & Brown (1967); Campbell (1971)
Summer NAO values	Negative	High summer NAO values lead to higher temperatures and lower rainfall during the summer months, of which both have been shown to negatively impact trout populations.	Jonsson & Jonsson (2011)

in reduced growth rates and future fecundity, increased risk of infection through external physical damage and ultimately increased mortality (Thorstad *et al*., 2015; Halttunen *et al*., 2017; Thorstad & Finstad, 2018; Serra-Llinares *et al*., 2020).

While the Atlantic salmon aquaculture industry has investigated some means of environmental mitigation, such as biocides and biological treatments (i.e. the use of cleaner fish (Gonzalez & de Boer, 2017)), increased salmon louse densities are still evident in wild salmonid populations in areas of intensive aquaculture (Shephard *et al*., 2016; Thorstad & Finstad, 2018; Moore *et al*., 2018; Karbowski *et al*., 2019). With the projected increase of net-pen salmon aquaculture, increased salmon lice densities and/or an increase the geographic distribution of high lice densities can be expected. The evidence of the study presented here is that this will pose an additional threat to wild sea trout communities.

This study has also demonstrated that there are relationships between sea trout populations, the annual biomass production of salmon aquaculture net-pens and climatic variables, particularly sea temperature and rainfall. Previous research has already shown a relationship between sea temperature and rainfall and salmon lice populations and the subsequent impacts on sea trout populations. For example, several studies have reported that salmonids host higher salmon lice densities, and have lower body condition as a result, during years that are warmer and drier (Shephard *et al*., 2016; Collins *et al*., 2020). Additionally, there is some evidence that the dispersal ranges of salmon lice will change and most likely increase as sea temperatures increase (Crosbie *et al*., 2020).

Due to the accelerated rate of climate change and expected increase in temperatures and more extreme weather patterns, sea trout populations will be exposed to major climatic shifts in sea temperatures and rainfall levels. When these changes in the natural environment are combined with the negative impacts of the expanding net-pen aquaculture industry, the effects on wild sea trout populations will become significantly more damaging. Therefore, the need to find effective mitigation methods to minimize the negative impacts of aquaculture is paramount in the successful management and conservation of sea trout populations.

Chapter 4: The influence of aquaculture unit proximity on the pattern of *Lepeophtheirus salmonis* infection of anadromous *Salmo trutta* populations on the Isle of Skye, Scotland

* Note: This chapter is published in the Journal of Fish Biology

Abstract

A total of 230 anadromous *Salmo trutta* (brown trout) were sampled in five sheltered coastal fjords (or sea lochs) on the Isle of Skye, Scotland in 2016 at varying distances from active *Salmo salar* (Atlantic salmon) farms. Statistical models were developed to investigate potential correlations between *Lepeophtheirus salmonis* (salmon lice) burdens on *S. trutta* hosts and their proximity to *S. salar* farm cages. Significant correlations were found between lice burdens and fish fork length and proximity to the nearest *S. salar* farm. The probability of the presence of *L. salmonis* on fish hosts increased with fish host size and with distance from the nearest *S. salar* farm, however, total lice burdens were highest in fish sampled near *S. salar* farms, and declined with distance. The proportion of different life cycle stages of *L. salmonis* were also dependent on *S. salar* farm proximity, with higher juvenile lice numbers recorded at sites near *S. salar* farm cages. These results highlight the complexity of the relationship between *S. trutta* and *L. salmonis* infections on wild fish, and emphasise the requirement of further research to quantify these effects to better inform conservation and management strategies, particularly in areas of active *S. salar* farm facilities.

4.1 Introduction

Migration, the spatial movement of an animal to and from a specific area is commonly exhibited by a wide variety of different taxa (Bohlin *et al*., 2001; Acolas *et al*., 2008; Chapman *et al*., 2011). The benefits that may arise from migration include greater access to resources, which frequently result in increased growth rate and fecundity (Eldøy *et al*., 2015). Large scale movements are exhibited by diadromous salmonids, such as *Salmo trutta* L. 1758 (brown trout) and *Salmo salar* L. 1758 (Atlantic salmon). Following a variable time period in fresh water, a subset of most *S. trutta* populations will smolt and undertake a seaward migration (Jonsson & Jonsson, 2011; Thorstad *et al*., 2016). This enigmatic behaviour is thought to occur only when the benefits of the migration (increased resources, fecundity, etc.) outweigh the costs (increased predation, exposure to disease, etc.) to the individual in the marine environment (Bohlin *et al*., 2001; Jonsson & Jonsson, 2011; Thorstad *et al*., 2016).

There is strong evidence that salmonid populations are in decline in many areas, including the UK, Europe, and Canada (Ford & Myers, 2008; Middlemas *et al*., 2013; Thorstad *et al*., 2015). Although this trend is difficult to quantify because of the logistical problems associated with sampling fish populations that travel such large distances (ICES 2016), it is apparent in rivers with long term count data, as well as in those with historic rod catch records (Gross *et al*., 1988; Gjelland *et al*., 2014; Gauld *et al*., 2016; ICES 2017). As a result of its cultural and economic importance considerable previous research has focused on the challenges facing *S. salar* populations (Limburg & Waldman, 2009). In contrast, considerably less attention has been given to the causes of decline of *S. trutta* (Drenner *et al*., 2012; Eldøy *et al*., 2017, Glover *et al*., 2017).

It is well established that, during the marine stage of their life cycle, anadromous *S. trutta* gain benefits from access to increased resources, but they are also exposed to increased costs, such as disease and predation, which can result in high levels of mortality (Drenner *et al*., 2012; Gjelland *et al*., 2014). Thus any change to the relative costs and benefits of marine migration have the potential for significant impact on anadromous populations. This has led to speculation that changes in marine migration costs might be contributing to the decline in anadromous *S. trutta* (Gjelland *et al*., 2014; Jennings *et al*., 2016).

One suspected contributing source of mortality that may have increased in recent years is the potential for infestation by *Lepeophtheirus salmonis* (Krøyer, 1837), a naturally occurring sea louse parasite that feeds on the mucus, tissue, and blood of their hosts, primarily salmonids (Boxaspen, 2006; Fast *et al*., 2007; Thorstad *et al*., 2015). Research has demonstrated that *L. salmonis* are responsive to changes in sea temperature, light and salinity levels, however, their responses vary depending on their life stage (Johnson & Albright, 1991; Thorstad *et al*., 2015). Survival rates of the parasite decline with decreasing salinity levels resulting in lower *L. salmonis* densities in areas with brackish conditions relative to densities found in areas with higher salinity levels (Bricknell *et al*., 2006; Rees *et al*., 2015).

The complex *L. salmonis* life cycle can be divided into eight developmental stages: two larval napulii phases that are planktonic, one copepodite phase that is also planktonic and free floating but must attach to a host, two chalimus phases (when the lice are able to begin feeding on their host), two pre-adult phases, and a final mature or reproductive phase (Fast *et al*., 2007; Gjelland *et al*., 2014; Thorstad *et al*., 2015). Beginning at the pre-adult phases, *L. salmonis* are able to move on the body surface of their host and can actively swim for short distances (Thorstad *et al*., 2015). The planktonic stages can be carried by wind-driven and tidal currents (Costello, 2009; Asplin *et al*., 2014).

High *L. salmonis* burdens can lead to increased osmoregulatory stress and eventual mortality in salmonids (Middlemas *et al*., 2013; Taranger *et al*., 2015; Thorstad *et al*., 2015). The incidence of *L. salmonis* on wild salmonids has increased since the 1960s and has been linked with the development of commercial *S. salar* farming (Thorstad *et al*., 2015).

In 2016, the international commercial aquaculture industry produced 1.5 million tonnes of *S. salar* and the industry has continued to grow (OECD, 2018). Previous research has suggested that expanding coastal *S. salar* farming in the UK, Norway, and Canada could lead to an increase in the densities of infective *L. salmonis* in coastal areas (Boxaspen, 2006; Gargan *et al*., 2012; Thorstad *et al*., 2015; Arechavala-Lopez *et al*., 2016; Shephard *et al*., 2016).

The observed increase in densities of infective *L. salmonis* on wild *S. trutta* populations has been linked with high densities of *S. salar* in marine farm cages, which provide *L. salmonis* with a large, easily accessible population of host species and allow them to feed

and reproduce successfully if left untreated (Salama *et al*., 2013). Open-net cages allow for the dispersion of free-floating *L. salmonis* from the cages and into the surrounding area, thus increasing their abundance in the surrounding ecosystem (Amundrud & Murray, 2009).

Coastal zones, frequently used for rearing *S. salar* in cages particularly in western Norway and Scotland, are also important feeding grounds for migratory *S. trutta* post-smolts (Jonsson & Jonsson, 2011). This habitat overlap has the potential to expose individual wild *S. trutta* to unnaturally elevated levels of *L. salmonis* parasites, and could thus lead to higher than natural lice infestations (Costello, 2009; Asplin *et al*., 2014; Thorstad *et al*., 2015; Gargan *et al*. 2012).

Research in Scandinavia, North America, and the UK has demonstrated that in areas where *S. salar* farms are present, a higher abundance of lice can be found in the water column and that wild salmonids are more heavily infected by *L. salmonis* (Gargan et al., 2012; Rees *et al*., 2015; Thorstad *et al*., 2015).

On the west coast of Scotland, similar trends have been observed in local salmonid populations. In a study in Loch Torridon, Penston & Davis (2009) reported that the number of gravid (or egg-bearing) *L. salmonis* found on farmed *S. salar* was "significantly correlated with the densities of *L. salmonis* copepodites in the water column". Middlemas *et al.* (2013) reported that the proportion of wild *S. trutta* with high *L. salmonis* infestations was significantly correlated to proximity of individual hosts to *S. salar* farms, and to fish length across the west coast of Scotland. Similarly, Shephard *et al*. (2016) showed that higher levels of *L. salmonis* infection were more commonly found on *S. trutta* which were captured closer to *S. salar* farm cages in Scotland and Ireland. Although knowledge of the dispersion rates and transmission locations of *L. salmonis* populations to wild salmonids is improving, there is still an urgent need for more information on the infection rates of *L. salmonis* in wild *S. trutta* in near-shore coastal habitats to provide further insight into the impacts of *S. salar* aquaculture on wild salmonid populations in Scotland (Middlemas *et al*., 2013).

Commercial *S. salar* farming began in Scotland in the 1960s and has continued to expand over time on northern and western coasts of the country (Ellis *et al.*, 2016). In 2016, a total of 162,817 tonnes of farmed *S. salar* were produced in Scotland and valued just below £600 million (Kenyon & Davies, 2018). The Scottish Government is encouraging the

growth of the industry, hoping to increase production to 210,000 tonnes by 2020 (Kenyon & Davies, 2018). This continued expansion of the industry suggests that wild *S. trutta* populations in Scotland may face increased pathogen exposure as more *S. salar* farms are built.

Currently, the Isle of Skye on the west coast of Scotland supports over ten active *S. salar* farms and several inactive, or fallow, farms that have previously been in use. With the continued future expansion of both the production capacity of current *S. salar* farms and the number of active farm sites around the island, it is crucial to gain a better understanding of salmonid behaviour in these shared habitats, as well as the impacts of *L. salmonis* infection burdens on an already declining wild *S. trutta* population.

Using anadromous *S. trutta* populations that were captured in five sheltered coastal inlets (from here on referred to as sea lochs) on the Isle of Skye (West Scotland) (Fig 4.1), the relationships between *L. salmonis* burdens on individual fish hosts and sampling site proximity to active *S. salar* farms were investigated.

4.2 Materials and Methods

4.2.1 Sampling

Five sea lochs, located around the Isle of Skye (lochs Snizort, Slapin, Portree, Eishort, and Harport) were sampled between April and September 2016 (Fig 4.1 & Table 4.1). The sites varied in their distance from active *S. salar* farms from 3 km (Loch Portree) to 48 km (Loch Eishort).

All *S. trutta* were caught using a combination of seine and fyke netting techniques in the tidal zones of each sea loch. The netting method used was dependent on site accessibility.

Seine netting was carried out at lochs Slapin and Snizort on a falling tide. A seine net of 30 m length and 20 mm mesh size was used at Loch Slapin and another seine net of 50 m length of and 20 mm mesh size was used at Loch Snizort. All captured fish were recovered with a large hand net and placed into a holding tank for processing.

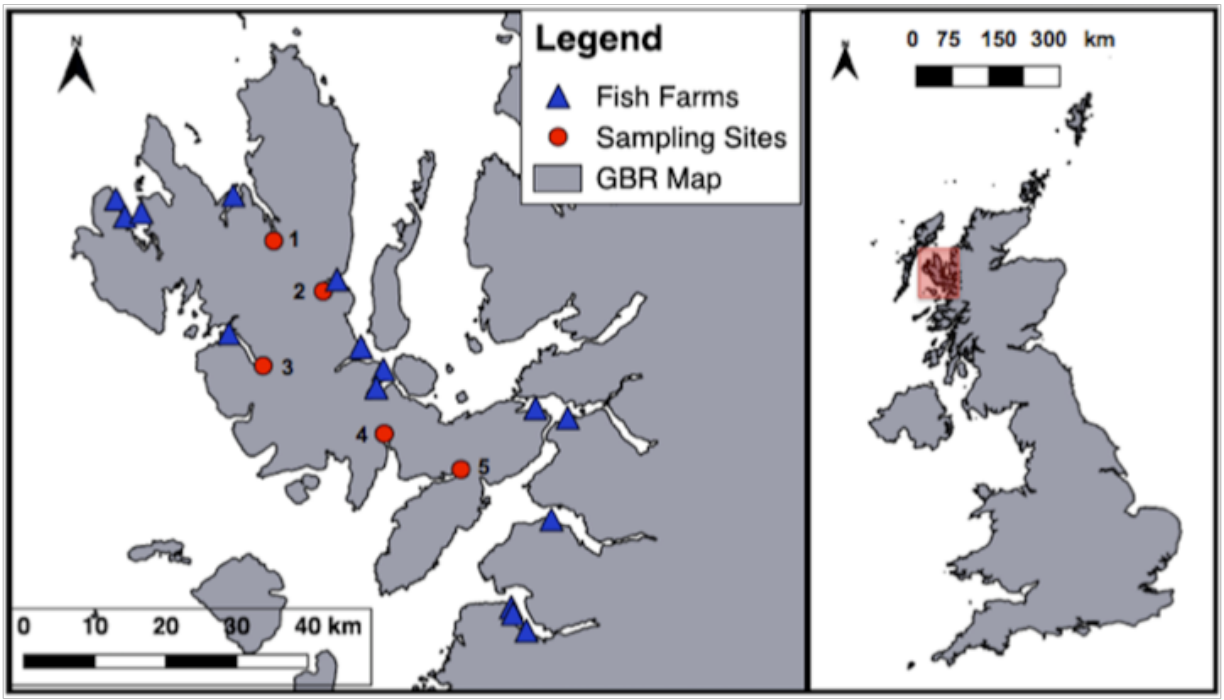


Figure 4.1. Map of study area, Isle of Skye, Scotland. Site 1: Loch Snizort; Site 2: Loch Portree; Site 3: Loch Harport; Loch 4: Loch Slapin; Loch 5: Loch Eishort.

Table 4.1. The locations of the five sea lochs and some additional information regarding size (in square kilometres, km^2), the type of netting method used at each site, the proximity of the site to the nearest active *Salmo salar* farm, the means and standard deviations of *Salmo trutta* fork length (mm), and lice counts of *Lepeophtheirus salmonis* (Juvenile, Mobile, Gravid Female, and Total Lice) observed at each site.

Loch	Corresponding River	Latitude	Longitude	Loch Size (km^2)	Netting Method	Farm Proximity (km)	Total No. of Fish Caught	Fork Length (mm) (mean±SE)	Juvenile Lice (mean±SE)	Mobile Lice (mean±SE)	Gravid Female Lice (mean±SE)	Total Lice (mean±SE)
Harport	Drynoch	57.29785	-6.31144	5	Fyke	8	36	217.7±10.5	2.1±0.9	0.2±0.1	0.2±0.1	2.5±0.9
Eishort	Eishort	57.18780	-5.84029	5	Fkye	48	27	236.3±11.2	3.0±1.8	1.7±0.4	2.3±0.6	7.0±2.1
Slapin	Strathmor	57.22107	-6.03199	7	Seine	46	88	227.8±8.5	1.5±0.5	1.3±0.2	0.8±0.2	3.7±0.7
Snizort	Snizort	57.45962	-6.32072	9	Seine	13	31	165.7±5.1	15.0±3.8	5.2±1.8	0.4±0.2	20.5±5.1
Portree	Varagill	57.39053	-6.20172	3	Fyke	3	44	216.1±10.0	0.1±0.1	0.1±0.1	0.1±0.1	0.3±0.2
All Sites	-	-	-	-	-	-	230	216.4±4.6	3.4±0.7	1.5±0.3	0.7±0.1	5.6±0.9

In Lochs Portree, Eishort, and Harport, two fyke nets (14 mm mesh size) were set in the mouth of each river, with one net placed in a downstream facing direction and one placed in an upstream facing direction. Leader nets were stretched to either bank to increase the chances of intercepting moving fish and guiding them into the net. The fyke nets were left in position for between two and four days and checked every 12 hours on a low tide. Any fish captured was placed into a holding tank for processing.

All captured fish were anesthetised using MS-222 (tricaine methanesulfonate) and their mass (g) and fork length (mm) were measured. From these, condition factor (k= mass/length^3) (Nash *et al*. 2006) was calculated. Visual *L. salmonis* counts were conducted on each fish, and the number of *L. salmonis* at each life stage (i.e. Juvenile, Mobile and Gravid Female) was recorded. All *L. salmonis* within the chalimus life stages were classified as "Juveniles", *L. salmonis* within the pre-adult, mature male and non-gravid female stages were classified as "Mobile", and reproducing female *L. salmonis* with attached paired egg strings were classified as "Gravid Females". All visual counts were conducted by the same researcher throughout the study to eliminate observer bias.

All fish were released back into the site they were captured from after they had sufficiently recovered from the anaesthetic and were able to swim independently.

Using *S. salar* farm locations available from the Scottish Government's aquaculture website (Scottish Government, 2018), the distance by sea from each sampling site to the nearest active farm site was calculated. The Scottish Government defines an active site as "an aquaculture site that has either actively produced fish or shellfish in the last 3 years or which is fallow as a part of a planned production cycle" (Scottish Government, 2018).

4.2.2 Statistical Analysis

To investigate the relationship between *L. salmonis* burdens on individual *S. trutta* hosts, five models were developed. Firstly, drivers of total *L. salmonis* burden were explored and secondly, drivers of life stage specific *L. salmonis* burden were investigated. R statistical software (R Core Team, 2017) and packages AICcmodavg (Mazerolle, 2016), effects (Fox, 2003), ggplot2 (Wickham, 2009), glmmADMB (Fournier *et al*., 2012), lattice (Sarkar, 2008), lme4 (Bates *et al*., 2015), multcomp (Hothorn *et al*., 2008), plyr (Wickham, 2011),

pscl (Zeileis *et al*., 2008), and R2admb (Bolker *et al*., 2016) provided the platform for all data analyses.

4.2.2.1 Total abundance of *L. salmonis*

Due to the relatively high numbers of fish that were found to be uninfected by *L. salmonis* (52%), the lice burden on individual *S. trutta* was examined using mixed effects models designed to handle zero-inflated data, classified as data made up of more than 25% zeros (Jansen *et al*., 2012; Zuur & Ieno, 2016). A binomial mixed effects model was created using the lmer4 and lattice packages to identify the factors that were influencing the presence or absence of *L. salmonis* on *S. trutta.* A second truncated negative binomial mixed effects model was created using the packages R2admb and glmmADMB to determine which covariates impact the *L. salmonis* burdens found in the positive non-zero count data of the study.

In both models, the presence or abundance of *L. salmonis* was the primary response variable, while fish length (mm), *S. salar* farm proximity (km), condition factor (k) were treated as covariates. A maximum statistical model including all covariates, their interactions, and also netting method as a random variable was created. A minimum adequate model was generated by a process of significance testing between models (ANOVA) and the sequential backward elimination of non-significant terms. The final model selected was the simplest model containing only significant predictors of the primary response variable, which was within two units of the lowest AIC value (Zuur & Ieno, 2016).

4.2.2.2 Life stage specific *L. salmonis* burden

Three life stage specific maximum GLM statistical models including the covariates and their interactions were created for each of the three broad life stages of *L. salmonis.* The life stage specific burden of *L. salmonis* (i.e. “Juvenile”, “Mobile”, and “Gravid Female”) was the primary response variables, whilst *S. salar* farm proximity (km) and total *L. salmonis* burden per individual host fish were treated as covariates. The final model for each life stage was selected using ANOVA significance testing to remove non-significant terms and ultimately determine the simplest model using AIC values.

Statistical analysis of this dataset ensured that model assumptions were met and collinearity was checked to identify covariates that were highly correlated. Highly correlated covariates, such as mass (g), were removed from further analysis to avoid replication of variation.

4.3 Results

A total of 230 fish were sampled from five sites (Table 4.1). Across all sites, *S. trutta* had a mean length of 216.4 ± 4.6 mm (Mean ± Standard Error) and a mean total parasite load of 5.6 ± 0.9 *L. salmonis* individuals per fish (Table 4.1). Overall, the mean numbers (Mean ± Standard Error) of juvenile, mobile, and gravid female lice per fish were 3.4 ± 0.7, 1.5 ± 0.3, and 0.7 ± 0.1 respectively (Table 4.1).

The binomial mixed effects model returned significant relationships between the presence of *L. salmonis* on individual *S. trutta* and *S. salar* farm proximity (km) and fish length (mm) (Table 4.2). The probability of an individual *S. trutta* being infected with *L. salmonis* was positively related to the distance to an active farm ($P < 0.001$) (Fig 4.2). Additionally, the model showed that the probability of *L. salmonis* presence on *S. trutta* was positively correlated to the length of a fish ($P < 0.001$) (Fig 4.3). Thus there was a higher probability of finding *L. salmonis* on larger fish and on fish that were further away from a *S. salar* farm.

The truncated negative binomial model indicated that *S. trutta* hosts that were infected with *L. salmonis* were more likely to have higher lice burdens in areas nearest to *S. salar* farms, and that burden declined with increasing distance from the nearest farm ($P < 0.01$) (Fig 4.4).

The three life stage specific GLM models determined that the proportions of different life stages of *L. salmonis* contributing to the total lice burden on *S. trutta* were significantly influenced by the proximity of sampling sites to the nearest *S. salar* farm (Fig 4.5).

4.3.1 Juvenile Life Stage

The proportion of juvenile *L. salmonis* was significantly influenced by an interaction between the total lice burden of *L. salmonis* on an individual fish, and the proximity of the

Table 4.2. (a) Mixed effects model output identifying significant correlations between zero inflated *Lepeophtheirus salmonis* count data and the length of sampled *Salmo trutta* hosts and their proximity to *Salmo salar* farms; (b) General linear model output demonstrating how the proportion of various *L. salmonis* life stages on *S. trutta* is significantly correlated to the host's proximity to the nearest fish farm and to the total *L. salmonis* on *S. trutta* hosts

(a) Mixed Effects Models			
	Estimate (SD)	**z-score**	**P-value**
Binomial			
Intercept	-0.156 (0.150)	-1.041	0.298
Farm Proximity (km)	0.771 (0.151)	5.12	<0.001
Fork Length (mm)	0.648 (0.174)	3.725	<0.001
Truncated Negative Binomial			
Intercept	3.524	8.95	<0.001
Farm Proximity (km)	-0.022 (0.007)	-3.06	<0.001
Fork Length (mm)	-0.002 (0.001)	-1.42	0.155
(b) General Linear Models			
Proportion of Juvenile Lice			
Intercept	-0.925 (0.143)	6.468	0.993^{-11}
Farm Proximity (km): Total Lice	0.001 (0.000)	-11.129	<0.001
Farm Proximity (km)	-0.053 (0.138)	-0.005	<0.001
Total Lice	-0.019 (0.003)	-6.57	<0.001
Proportion of Mobile Lice			
Intercept	-1.461 (0.106)	-13.755	<0.001
Farm Proximity (km)	0.011 (0.003)	3.651	<0.001
Proportion of Gravid Female Lice			
Intercept	-0.925 (0.143)	-6.122	<0.001
Farm Proximity (km)	0.031 (0.007)	4.689	<0.001
Total Lice	-0.049 (0.006)	-7.546	<0.001

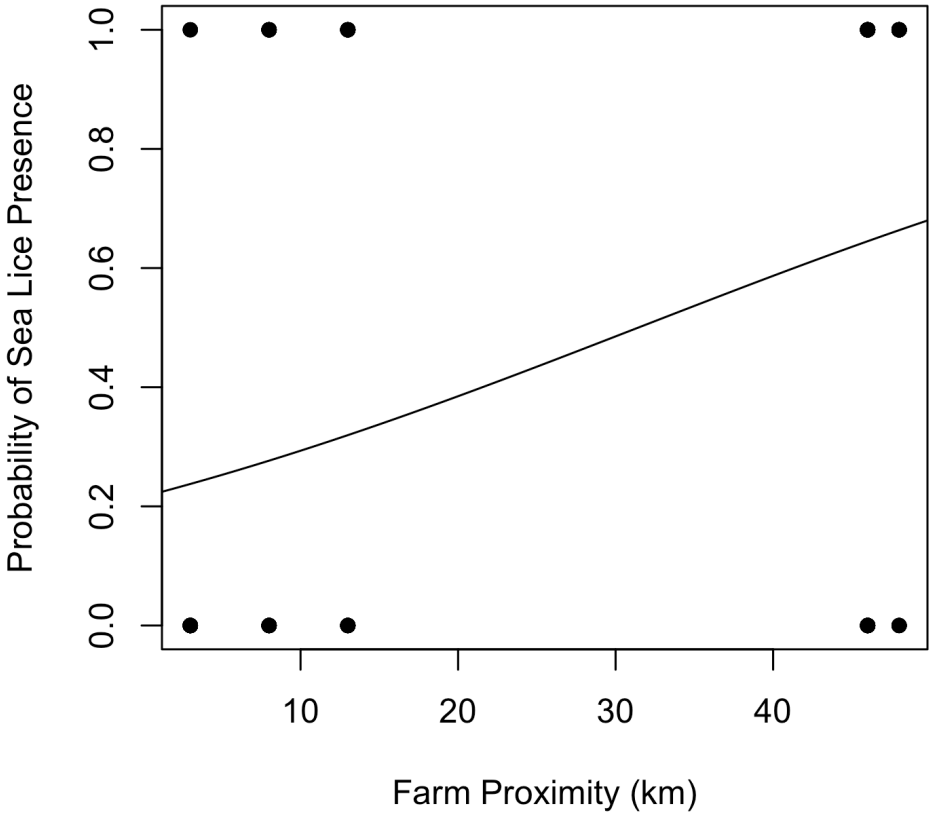


Figure 4.2. A probability distribution curve depicting the significant correlation between the likelihood of *Lepeophtheirus salmonis* presence and *Salmo salar* farm proximity (km) ($P < 0.001$).

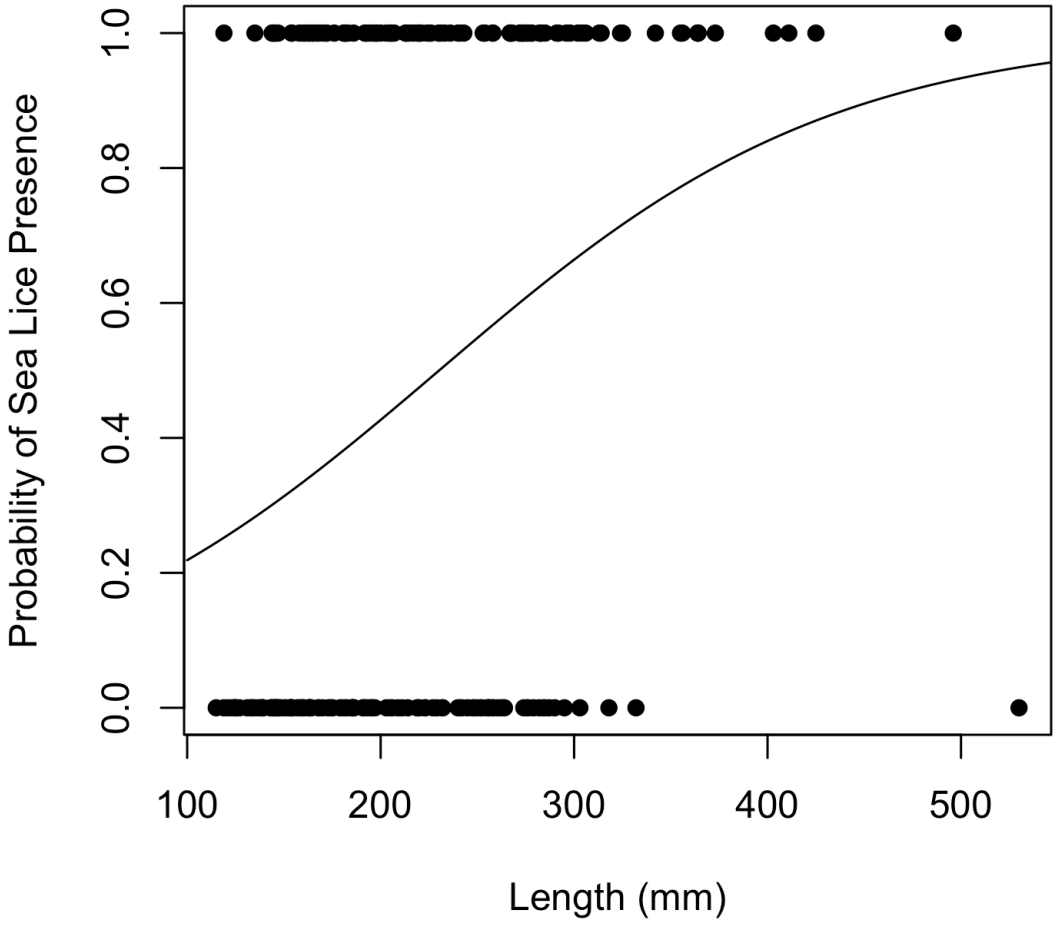


Figure 4.3. A probability distribution curve depicting the significant correlation between the likelihood of *Lepeophtheirus salmonis* presence and *Salmo trutta* fork length (mm) ($P < 0.001$).

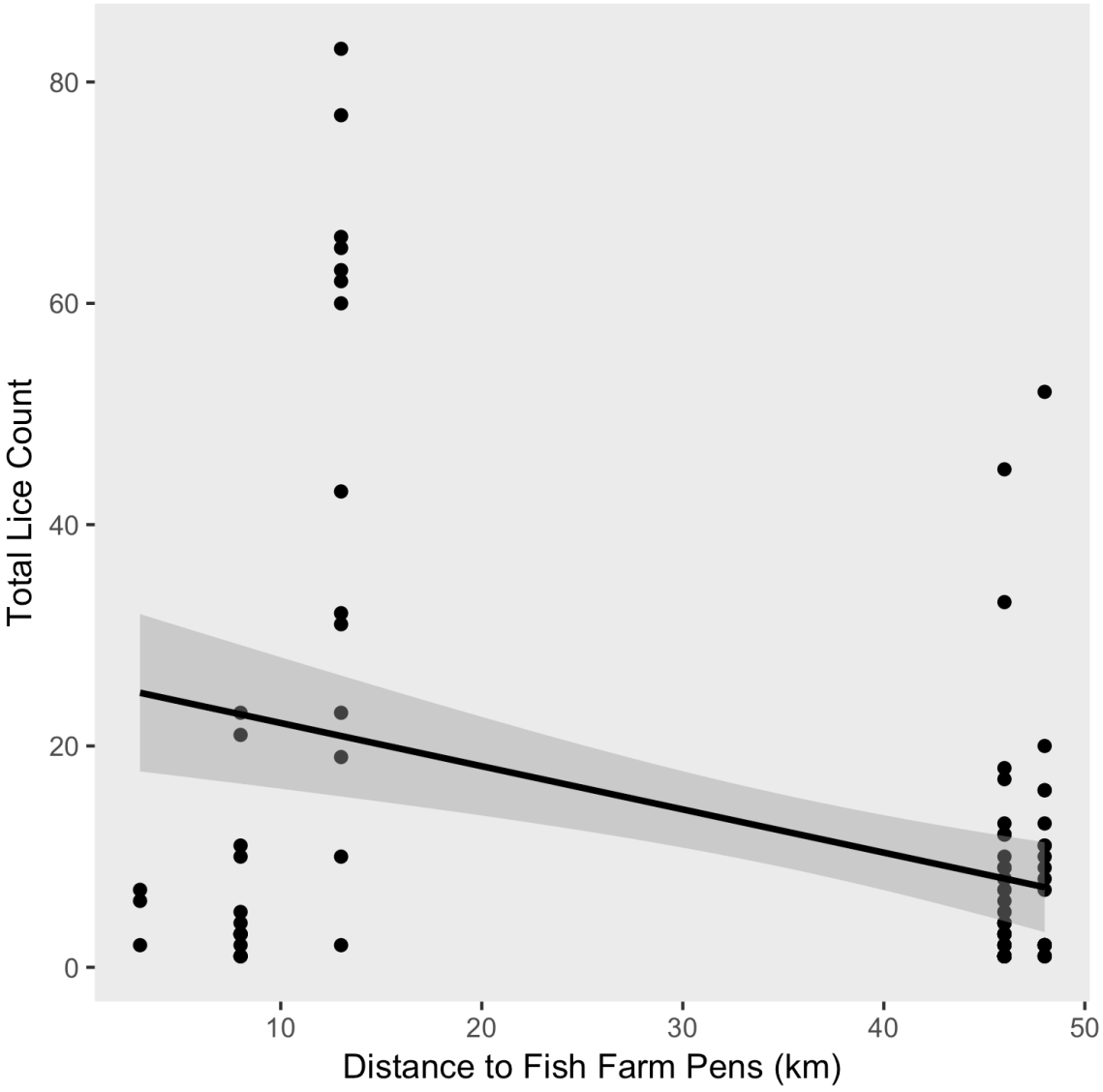


Figure 4.4. The significant correlation identified by a hurdle model between total *Lepeophtheirus salmonis* abundance found on *Salmo trutta* when *L. salmonis* abundance >0 and the proximity of the captured fish to the nearest *Salmo salar* farm (P = 0.03).

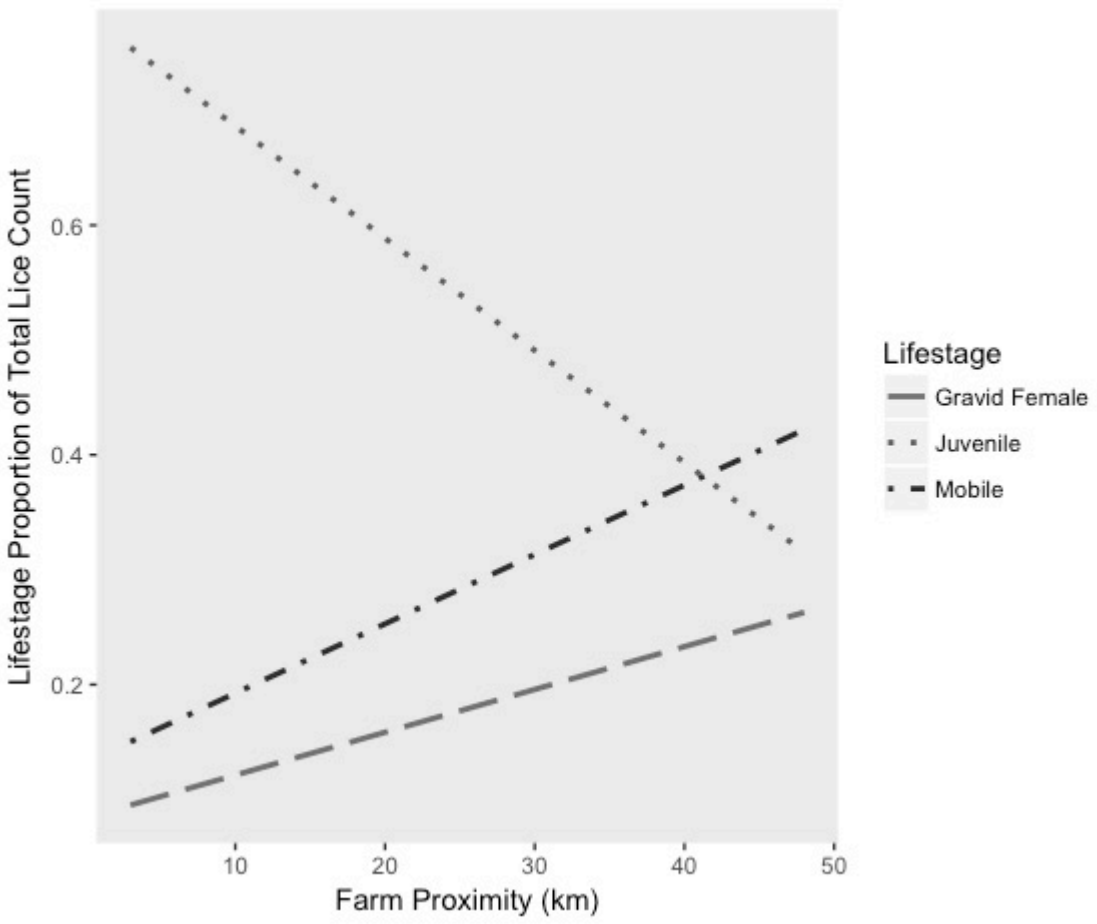


Figure 4.5. The proportions of different *Lepeophtheirus salmonis* life stages contributing to total lice abundance on *Salmo trutta* in relation to *Salmo salar* farm proximity (km).

nearest *S. salar* farm (P<0.001) (Fig 4.6). This interaction was typified by a relationship where, on fish captured within close proximity to *S. salar* farms and, when the lice burden on the fish was high, juvenile lice comprised a low proportion of the total lice burden. This relationship was reversed when total lice burden on fish, captured close to *S. salar* farms, was low; i.e. juvenile lice formed a relatively higher proportion of the lice burden.

Furthermore, when individual fish were sampled further from *S. salar* farms, the proportion of juveniles would also fluctuate based on the total lice burden of *L. salmonis*. Fish with lower lice burdens would have fewer juvenile lice, while fish with a high lice burden would have a high proportion of juveniles.

4.3.2 Mobile Life Stage

A significant and positive relationship between the proportion of mobile *L. salmonis* on *S. trutta* hosts and *S. salar* farm proximity was also identified (P<0.001) (Table 4.2). The model results indicated that proportion of mobile lice contributing to the total lice burden increased with increasing distance from *S. salar* farms.

4.3.3 Gravid Female Life Stage

The model indicated that individual fish sampled at increasing distances from *S. salar* farms had a higher proportion of gravid *L. salmonis* females (P <0.001) (Table 4.2). Additionally, a significant and negative relationship was found between the proportion of mature gravid females and the total lice burden found on sampled *S. trutta* (P <0.001). This indicated that as the total burden of *L. salmonis* increased, the number of gravid females comprising the total lice burden declined.

4.4 Discussion

The probability of finding *L. salmonis* present on a host fish significantly increases with fish length. Larger fish will often have higher lice burdens simply due to the increased surface area available to feeding *L. salmonis* (Tucker *et al*., 2002; Costello, 2009; Middlemas *et al*., 2013) and there is an increased likelihood of *L. salmonis* encountering a fish with a larger surface area. Migratory *S. trutta* occupy coastal areas during the marine phase of their life cycle as they try to maximise individual growth rates. Increases in the

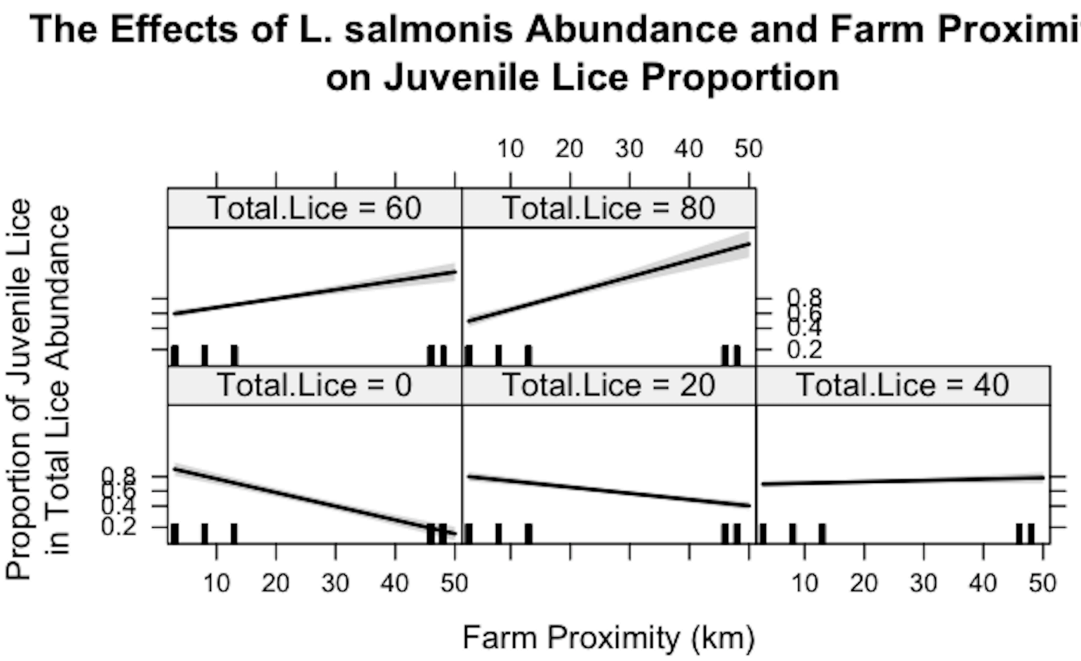


Figure 4.6. The significant interaction between total *Lepeophtheirus salmonis* abundance and *Salmo salar* farm proximity and their effects on the proportion of juvenile *L. salmonis* within the count sample.

amount of time spent in these environments has the potential to amplify the number of encounters an individual fish has with *L. salmonis*, as well as the host's overall louse burden.

The proximity of *S. salar* farms had a significant impact on both the probability of infection with *L. salmonis* and on the total lice burden of infected *S. trutta*. There was a higher probability of finding *L. salmonis* present on *S. trutta* that are further away from the nearest *S. salar* farm. Because *L. salmonis* is a naturally occurring parasite, varying abundances of this ectoparasite can also be found in coastal areas where *S. salar* farms are not present (Urquhart *et al*., 2010; Jansen *et al*., 2012; Thorstad *et al*., 2015). Large, shallow, and sheltered sea lochs that *S. trutta* have been shown to use as feeding grounds are also capable of supporting native *L. salmonis* populations due to the continuous presence of host species utilising the same area (Costello, 2009; Urquhart *et al*., 2010).

The study sites Loch Slapin and Loch Eishort have similar geographic characteristics (large, shallow, and sheltered) and are located 46 and 48 km, respectively, away from the nearest *S. salar* farm. Historically, there was an active *S. salar* farm in Loch Slapin, but the site was closed around eight years prior to this study due to high levels of lice infestation that the farm operators were unable to control. The farm site has remained fallow ever since and based on previous studies suggesting that *L. salmonis* levels are significantly reduced after a fallowing period of six months (Bron *et al*., 1993; Rae, 2002; Costello, 2006), it is unlikely that the history of this site would have an impact on the levels of *L. salmonis* observed during this study.

An average of 3.7 ± 0.7 total *L. salmonis* individuals/fish were reported in Loch Slapin in this study and 7.0 ± 2.1 total *L. salmonis* individuals /fish in Loch Eishort. A literature review by Thorstad *et al*. (2015) reported peak natural *L. salmonis* levels in areas without *S. salar* farms as 4-8 total lice per individual *S. trutta* in summer and autumn months. This, and because of the likely favourable environmental conditions for supporting *S. trutta* hosts and their *L. salmonis* populations within Lochs Slapin and Eishort, it is highly possible that for these sites, *L. salmonis* densities represent lice levels which would occur in naturally, without the influence of *S. salar* farms.

In contrast to the high probability of finding one or more *L. salmonis* on *S. trutta* sampled in areas further from *S. salar* farms, higher abundances of *L. salmonis* were found on host

individuals that were captured in areas that are geographically closer to *S. salar* farm pens. These findings are similar to those of a number of other studies (e.g. Parker & Margolis, 1964; Middlemas *et al*., 2013; Shephard *et al*., 2016). For example, a modelling study by Gillibrand & Willis (2007) reported a similar result, in that copepodid abundance on wild fish reached a maximum between 7 and 12 km from the *S. salar* farm source. However, the distance at which maximum infection rate occurs will vary depending on topography and wind-driven and tidal currents (Costello 2009).

High lice loading is particularly apparent in Loch Snizort in this study, where an average of 20.5 ± 5.1 *L. salmonis*/fish was recorded and the nearest *S. salar* farm is 13 km away. A burden of *L. salmonis* of this magnitude is thought to have a direct impact on mortality in wild salmonids (Taranger *et al*., 2015). Taranger *et al*. (op. cit.) developed an index to assess *L. salmonis* burdens in relation to fish mass. The index used laboratory experiments to calculate the increased chance of mortality in both post smolts (<150g), and larger salmonids (>150g) based on the mass of the fish (g). Their results indicated that post smolts with 0.2- 0.3 lice/g of fish and larger salmonids with 0.05-0.10 lice/g of fish, carried a 50% risk of mortality. Additionally, they determined that if a post smolt had a burden of >0.3 lice/g and a larger salmonid had >0.15 lice/g, then those individuals had a 100% risk of dying.

The probability model of Taranger *et al*. (2015) has not been empirically tested in a field environment and therefore should not be viewed as a final answer to management questions on the critical loading level of salmonid lice abundance in the wild (Thorstad *et al*., 2015). For example, the average weight of the *S. trutta* sampled in Loch Snizort was 54.1 ± 5.9g, and the average number of *L. salmonis* on each fish was 20.5 ± 5.1, which equates to 0.38 lice/g. This value exceeds the threshold reported by Taranger *et al.* (2015), which leads to 100% lice related mortality in salmonids of less than 150 g in mass. In comparison, fish from Loch Slapin and Loch Eishort, where the nearest *S. salar* farm is more than 45 km away, had respective mean values of 0.02 lice/g and 0.04 lice/g. These levels are lower than the threshold predicted by Taranger *et al*. (2015) as increasing the probability of mortality in fish less than 150 g at all, but would, however, result in a 20% lice related mortality in fish weighing more than 150 g.

4.4.1 Life Stage Specific *L. salmonis* Burden

By looking at the life cycle stages of *L. salmonis* and their relative proportion as a part of the total lice burden, further information about the potential location of parasite transmittance between fish populations emerges. In this study, all stages of the *L. salmonis* life cycle are significantly influenced by the proximity of the sampled host individual to the nearest *S. salar* fish farm. However, differences in this relationship are evident between the proportion of juvenile *L. salmonis* and the proportions of mobile and gravid females that make up the total lice burden.

The relative proportions of juvenile *L. salmonis* consistently make up a large share of the total number of lice on *S. trutta* sampled near to *S. salar* farms, however, this ratio fluctuates depending upon the total lice abundance, and the host's proximity to a farm. This complex relationship highlights the variation of dispersion rates and distances that juvenile *L. salmonis* may disperse from their source. Previous studies demonstrated that increased *L. salmonis* abundance can be observed up to 30 km away from *S. salar* farms (Middlemas *et al.,* 2013; Rees *et al*., 2015).

Marine *S. salar* aquaculture production units in Scotland are commonly located in coastal areas, a habitat that is widely used by young smolt and post smolt *S. trutta* (Shephard *et al*., 2016). The open net pens which are used in these facilities allow free floating *L. salmonis* larvae to disperse from net pens by wind and tidal currents, and potentially come into contact with any wild fish in the area (Penston *et al*., 2008, Costello, 2009). Therefore, it could be argued that the habitats frequented by the young fish that were sampled in this study are often predisposed towards having higher juvenile lice densities because of the presence of *S. salar* farms which act as a key source of *L. salmonis* larvae (Penston *et al*., 2008; Penston & Davies, 2009; Thorstad *et al*., 2015).

Brooks (2005), however, reported a higher probability of finding the infective stages of *L. salmonis* at a distance of 7-10 km from their source (*S. salar* farms) as a result of a combination of the time taken to develop to the infectious stage and dispersion of lice larvae via water currents. Thus local environmental conditions (e.g. salinity, temperature, topography, currents and tides, etc.) may all affect probability of infection and infection rate. While the majority of research has demonstrated that the transmission of lice at the juvenile stage is more likely to occur close to the source of the population (i.e. *S. salar* farms), it is possible that, in areas of high louse density, a portion of the lice in their larval stage would be carried away by local environmental conditions before they are developed enough to attach to a host (Brooks & Stucchi, 2006; Penston & Davies, 2009). Several

modelling studies have demonstrated that *L. salmonis* dispersion can be explained by wind and tidal currents which can carry the lice up to 30 km in Scottish loch systems (Krkošek *et al*., 2005; Middlemas *et al*., 2013; Salama *et al*., 2013) and up to 97 km in Norwegian fjords (Asplin *et al*., 2014).

The relationships between the mobile and gravid female life stages are less complex. There is a certain amount of variation between the ratio of each life stage relative to the total burden of lice on an individual fish sampled near a *S. salar* farm. As the distance from the nearest *S. salar* farm increases, however, the proportion of mobile lice also increases. The proportion of gravid females follows a similar trend as it increases with distance from *S. salar* farms. Additionally, the ratio of gravid females is higher on fish with low lice abundance, but declines slightly when the total lice abundance increases. These trends would suggest that the more mature stages of the *L. salmonis* life cycle comprise a larger proportion of the total lice burden in areas more distant from *S. salar* farms.

The varying ratios of different life stages found across the large spatial area of this study could be explained by the speed of progression through successive life stage moults which can occur over a series of weeks or months, depending on climatic conditions (Boxaspen, 2006). *S. trutta* sharing coastal habitats with *S. salar* fish farms would be exposed to the juvenile stages of lice in those environments, which would then contribute to the high proportion of juveniles found in the total lice burdens (Penston & Davies, 2009). As infected *S. trutta* are likely to move around coastal areas, as part of their migration strategy, the surviving lice would continue to feed and reach sexual maturity, therefore contributing more mobile lice to the total ratio found on more mature fish that have moved away from the source of infection.

There are other possible explanations for the observed patterns of life stage *L. salmonis* infections on fish in this study. One possibility is that those fish that acquire the high infection rate documented closer to farm sites may well have a higher probability of mortality if juvenile *L. salmonis* develop to the more damaging mobile stages (Thorstad *et al*., 2015). High levels of mortality would not be detected in this study design. Thus the higher relative ratio of the mobile *L. salmonis* stages further away from farms may represent fish that have been previously subjected to low juvenile *L. salmonis* infection rates that exert a lower mortality rate.

Results from this study have provided further insight into the complex relationships between *S. trutta* and *L. salmonis* populations. As the *S. salar* aquaculture industry continues to expand in Scotland, it is critical to better understand farming impacts, such as disease transfer, on already threatened wild salmonid communities.

This study did not include the effects of temperature, current, wind, salinity, or early fresh water entry on *L. salmonis* loading. Additionally, there is little information on the movement of *S. trutta* between sea lochs and the extent of their travel around the coastlines of Scotland.

Future work in this field could include the tracking of *S. trutta* movement at varying ages in combination with modelling *L. salmonis* dispersion rates in Scottish sea lochs to determine the extent of transmission at stages of the *L. salmonis* life cycle in areas with different environmental and climatic factors. Such research would help elucidate the details of *L. salmonis* dispersal mechanisms between farmed and wild salmonid populations. Nevertheless, our data add to the empirical evidence that *L. salmonis* from farms can cause fatal infestations of wild *S. trutta* and highlight the importance of limiting *L. salmonis* abundance on farms to improve wild salmonid survival.

Chapter 5: Seasonal habitat use and aquaculture interactions of sea trout (*Salmo trutta*) post-smolts in neighbouring Scottish sea lochs

Abstract

Movements of anadromous brown trout (*Salmo trutta* L. 1758) (sea trout) in the marine environment are not fully understood. There is some evidence that sea trout prefer to spend large periods of time in near-shore coastal habitats, particularly young post-smolts during their first summer at sea. In Scotland, these fjordic types of habitats (referred to as sea lochs) are being used more often by the expanding Atlantic salmon (*Salmo salar* L. 1758) aquaculture industry as locations for open-net pen sites, increasing the exposure of wild salmonids in the same areas to pathogens and degraded habitats.

In this study, acoustic telemetry methods were used to gather data on the movements of 60 tagged sea trout post-smolts in two adjacent sea lochs, both in the presence and absence of an open-net pen site. A total of 46 individuals were detected on the receiver array. The study showed a variety of intra- and interpopulation post-smolt space use patterns within the receiver array over the course of the study. The majority of the detected post-smolts (72%) remained in their natal sea loch for the duration of the study and did not migrate into deeper water. The remaining 28% of the detected population migrated out of their natal sea loch, with some individuals migrating between the adjacent sea lochs and others migrating outside of the array but returning to their natal sea loch. Only five individuals (10%) were found to have left the array without returning over the duration of the study. Survival and migration range were not significantly correlated to fish size. A small percentage of the detected population (21%) were detected near the open-net pen site located in one of the lochs, but analysis demonstrated that there was not a significant difference between the amount of time these individuals spent near the open-net pens and the amount of time spent at receivers in the rest of the array, suggesting that sea trout populations are not actively attracted to aquaculture sites.

5.1 Introduction

The brown trout (*Salmo trutta* L. 1758) is a geographically widespread salmonid species that is known for its partial migration life history strategy (Jonsson & Jonsson, 2011). All trout begin their lives in freshwater, but research has demonstrated that a complex combination of genetic and environmental factors influence a trout's decision to adopt an anadromous life history, where an individual (hereafter, known as sea trout) will migrate from their natal river into the marine environment (Ferguson *et al*., 2019b). This shift in habitat coincides with increased foraging opportunities and the potential for enhanced fitness through increased fecundity resulting from greater body size at spawning for those migrating compared to the fish that remain in freshwater for the duration of their life (Aarestrup et al. 2014; Kristensen *et al*., 2019a). However, the marine environment also introduces additional costs to the migrating sea trout population, such as increased predation and risk of disease (Thorstad *et al*., 2016; Moore *et al*., 2018).

In recent decades, multiple European countries have reported that sea trout numbers have been in decline, with some populations classed as "vulnerable" (ICES, 2017; Evans & Harris, 2017; Höjesjö *et al*., 2017). There is much research that has identified the causes of the population decline in freshwater environments across Europe (such as habitat degradation (Aarestrup *et al*., 2014) and restricted access to spawning grounds due to barriers (Birnie-Gauvin *et al*., 2018)). Less is known about threats that anadromous individuals face in the marine environment, although research has suggested that marine mortality is having a significant impact on the observed declines (Thorstad *et al*., 2016).

Until recently, the movements of sea trout in the marine environment have been relatively undocumented given the difficulties of tracking aquatic animals in large bodies of water. Advances in acoustic telemetry technology have created better opportunities for research into the marine movements of sea trout. A small number of acoustic telemetry studies involving sea trout in Europe and Scandinavia have shown great spatial variability in their habitat usage (Aldvén & Davidsen, 2017). Some individuals migrate out to sea and along the coastline for several hundred kilometres away from their natal rivers (Kristensen *et al*., 2019b). Flaten *et al*. (2016) reported that 94% of post smolts were recorded at least 14 km away from their natal river mouth. But there is also evidence that points to many sea trout remaining in close proximity to their river of origin (Thorstad *et al*., 2016). Several studies have suggested that anadromous sea trout make greater use of foraging sites in estuaries

than previously thought (Davidsen *et al*., 2014; del Villar-Guerra *et al*., 2014; Aldvén & Davidsen, 2017; Honkanen *et al*., 2019). Eldøy *et al*. (2015) demonstrated that veteran migrant sea trout spent 68% of their time in a Norwegian marine environment within 4 km of their river of origin.

From this body of research, it is thought that there is a dichotomy of spatial range by sea trout in marine habitats, potentially even within the same population. A study conducted by del Villar-Guerra *et al*. (2014) demonstrated that there was a split in migratory patterns exhibited by sea trout post-smolts originating from the same river in Denmark, with some individuals remaining in their natal fjord system for over 100 days, while another subset of individuals migrated out of the fjord within ~40 days. From this study, it was suggested that once sea trout enter the marine environment, they face a new decision on the adoption of migration strategies when they choose to remain within their natal fjord system or migrate to the open ocean. Ferguson *et al*. (2019b) reported a similar "continuum of migration" for sea trout populations where some individuals remain in more coastal estuaries (fish are referred to as "semi-anadromous"), while other migrate into the open ocean (fish are referred to as "anadromous").

Despite the studies on the movements of sea trout in the marine environment from elsewhere in Europe and Scandinavia, there is little information on the movements of UK sea trout once they leave their natal river. However, it is suspected from data that have been collected that sea trout are not using marine habitats similarly. Some studies have determined that young sea trout smolt populations from two Welsh rivers (the Rivers Conwy and Avon) move quickly out into the open sea (Moore & Potter, 1994; Moore *et al*. 1998), mimicking the movements of Atlantic salmon (*Salmo salar* L. 1758) that migrate directly out into deeper water upon leaving freshwater. Pemberton (1976) determined from extensive seine netting that Scottish sea trout will move out of their natal fjord-like systems (hereafter referred to by the vernacular term, sea lochs) during the summer in search of food before returning in the autumn. Migrating into more open water provides sea trout with larger and potentially more abundant prey items which would increase individual growth rates, however, larger predators are also found in these areas, increasing potential mortality levels due to predation (Thorstad *et al*., 2016).

Other studies have demonstrated that sea trout remain close to their natal river, preferring to forage in coastal sea lochs that provide more estuarine environments. Honkanen *et al*. (2019) reported that veteran migrant sea trout remained in the inner estuary of a large

Scottish sea loch system instead of seeking out deep-water habitats during the summer months. Middlemas *et al*. (2009) reported that of 48 detected post-smolts in their study, most stayed in close proximity to their natal river for the first 14 days after entering the marine environment and ultimately 37% of post-smolts remained in sea lochs less than 6 km from their natal river during the course of the study. This possible preference of sea loch habitat by sea trout, particularly young post-smolts (Aldvén & Davidsen, 2017), provides individuals with nutrient-rich environments where the osmoregulatory strain of adjusting to increased salinity is reduced and fewer large predators are present (Thorstad *et al*., 2016).

However, anthropogenic influence has altered these important sea lochs significantly in recent years, most notably with the rapid expansion of Atlantic salmon (*Salmo salar*) aquaculture in open net-pens in Scotland that are primarily located in sheltered sea lochs on the west coast (Middlemas *et al*., 2013; Shephard *et al*., 2016). Open net-pen (known hereafter as net-pens) aquaculture can negatively impact the surrounding marine wildlife and environment, resulting in increased pathogens, nutrients and chemicals entering into the ecosystem (Ford *et al*., 2012; Gonzalez & de Boer, 2017; Atalah & Sanchez-Jerez, 2020).

One of the more well-known and widespread threats in areas of intensive net-pen salmon aquaculture is *Lepeophtheirus salmonis,* (known hereafter as the salmon louse) a naturally occurring copepod crustacean ectoparasite that parasitises primarily on salmonids (Boxaspen, 2006; Middlemas *et al*., 2013). In low numbers, salmon lice cause minimal injury to their hosts, but high lice infections can lead to extensive damage to the skin and tissue of a host, impacting osmoregulatory function and increasing the likelihood of secondary disease or infection (Thorstad *et al*., 2015) Salmon lice have the potential to reach high densities in net-pens where there are large numbers of host species in small spaces. The larval stages can be carried out of the net-pens by tides and wind-driven currents into the surrounding coastal environment where they come into contact with wild fish in the area (Thorstad *et al*., 2015).

The potential overlap in coastal habitat use by sea trout and net-pen aquaculture has raised concerns about the negative influence of net-pen aquaculture on vulnerable wild sea trout (Moore *et al*., 2018). Middlemas *et al*. (2013) demonstrated that increased salmon lice levels could be observed in the water column up to 30 km away from net-pen aquaculture

sites, indicating that wild salmonids utilising these same areas are likely to come into contact with increased parasite densities than they would normally.

A wild sea trout with a high salmon louse infestation can suffer an overall decline in condition through external damage and reduced growth rate, which can lead to increased risk of predation and mortality (Thorstad *et al*., 2015). Halttunen *et al*. (2017) showed that the migratory behaviour of sea trout can be influenced by parasite loads, in that fish with high infection levels are more likely to return to freshwater early (prior to spawning) to rid themselves of the parasites, resulting in long term impacts on growth rates and fecundity. Research from Europe and Canada has suggested that sea trout population declines have been influenced by large salmon lice outbreaks derived from aquaculture facilities (Gjelland *et al*., 2014; Rees *et al*., 2015; Shephard *et al*., 2016; Thorstad & Finstad, 2018).

Despite the large body of evidence demonstrating that net-pen aquaculture acts as a strong driving factor behind large epizootic outbreaks of salmon lice and the subsequent negative impact on sea trout populations (Thorstad & Finstad, 2018; Wilson & Veneranta, 2019), there have been few studies to identify the physical behavioural interactions between wild sea trout and net-pens in Scotland. Although research suggests that a wide variety of wild fish can be attracted to aquaculture facilities, particularly in warmer climates (Machias *et al*., 2006; Demétrio *et al*., 2011; Uglem *et al*., 2014; Callier *et al*., 2018), less is known about wild salmonid-specific interactions with salmon net-pen aquaculture (Thorstad *et al*., 2012).

Furthermore, because there is limited understanding of the range of migration displayed by Scottish sea trout, it is unclear if the preferred habitat range of sea trout could be placing them at higher risk of salmon lice infection. For example, if sea trout post-smolts are choosing to remain in their natal sea loch instead of migrating out to sea but the sea loch is within the suspected 30 km “range of influence” of active net-pens, it is possible that the sea trout could face increased exposure to high salmon lice densities emanating from the net-pens.

To examine marine habitat use in sea trout, we used well tested acoustic telemetry techniques that can track the movements of fish in both marine and freshwaters (Crossin *et al*., 2017). A small transmitter that produces a coded sound signal at intervals is implanted into fish and acoustic receivers are used to log the presence of a fish as it passes within range of the receiver. Frequently multiple receivers are deployed as an array to be able to

determine patterns of fish movements or habitat use. This technique has been used in studies of migration patterns of Atlantic salmon (for Scottish examples see Honkanen *et al*., 2019; Lothian *et al*., 2018), and of sea trout in Scandinavia (Flaten *et al*., 2016; Eldøy *et al*., 2017; Kristensen *et al*., 2019a; Kristensen *et al*., 2019b).

Using acoustic telemetry, this study aims to address the following questions:

- Do Scottish sea trout post-smolts remain within their sea loch of origin during their first summer at sea? Or do they migrate out into the wider coastal marine environment
- Does fish length predict migration strategy or range?
- Are post-smolts attracted to net-pens at aquaculture facilities?
- Does the pattern of coastal habitat use by sea trout post-smolts change with time?
- Are populations of different catchments acting similarly in their use of coastal habitats?

5.2 Materials and Methods

This study was conducted in 2017 in Loch Greshornish (~5 km^2) (57°30.161′; 006°25.653′) and Loch Snizort Beag (~8 km^2) (hereafter referred to as Loch Snizort) (57°30.259′; 006°21.303′), two adjacent sea lochs located on the northern coast of the Isle of Skye on the west coast of Scotland (Fig 5.1). At the time of the study, Loch Greshornish hosted an active net-pen Atlantic salmon aquaculture facility with 12 pens, while Loch Snizort did not have any net-pens present. Environmental data collected by the net-pen facility in Loch Greshornish over the duration of the study (April-July), reported that salinity levels in the area ranged from 32.0 to 36.8 (32.7 ± 0.8, mean ± standard deviation) and sea temperatures ranged from 7.6 to 14.3 (10.7 ± 1.6, mean ± standard deviation).

Receivers capable of detecting acoustic transmitters operating at 69 kHz were deployed in an array designed to strategically monitor areas of particular interest, including coastal and estuarine tidal areas and surrounding the net-pens of the aquaculture facility in Loch Greshornish. The receiver mooring system used a series of weights, buoys and lines to secure the receivers and limit noise interference from the surface of the water (Fig 5.2) Across the study site, the majority of receivers were placed in “curtain” arrays, or lines, to

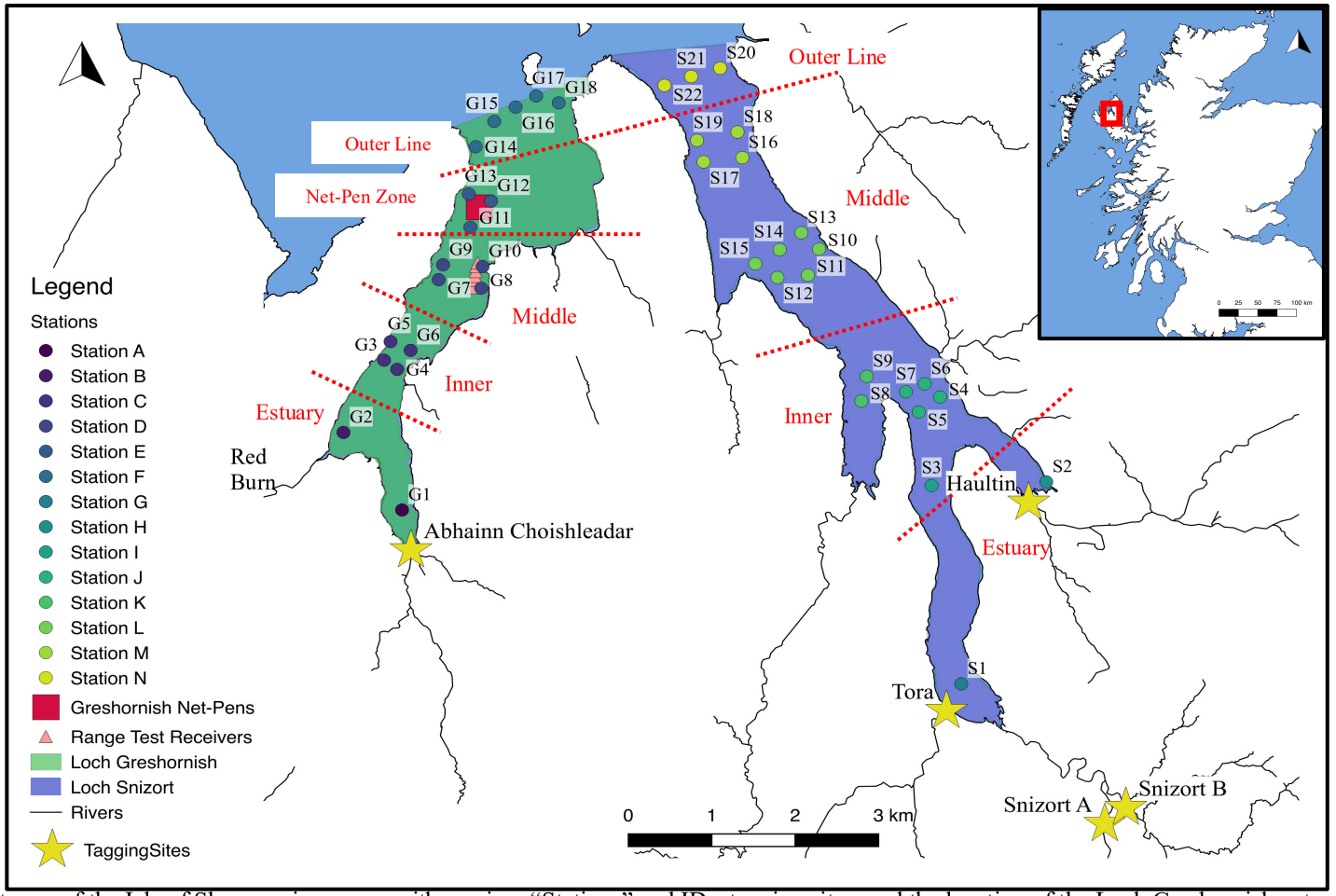


Figure 5.1. Insert map of the Isle of Skye receiver array with receiver "Stations" and IDs, tagging sites, and the location of the Loch Greshornish net-pen farm (identified as ■). Loch Greshornish (left) is highlighted in green. Loch Snizort (right) is highlighted in purple.

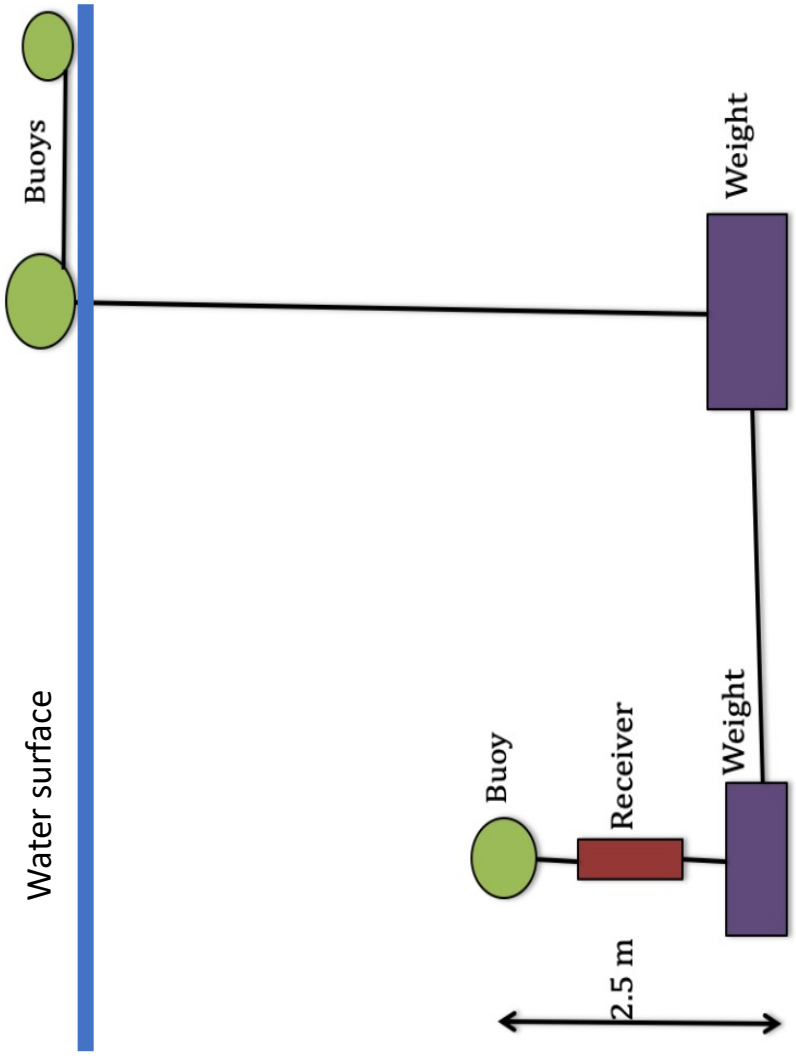


Figure 5.2. Receiver mooring system used in this study.

act as a series of gates that would provide the best detection coverage of tagged individuals as they moved through the loch. Furthermore, most of the curtain arrays were deployed as double lines to provide more fine scale data on the migration direction of a fish. The full acoustic receiver array comprised 40 Vemco receivers (29 VR2W, nine VR2TX and four VR2). Eighteen (18) receivers were deployed in Loch Greshornish and 22 were deployed in Loch Snizort. The receiver array was designated into sections ("estuary", "inner", "middle", "net-pen zone" and "outer line") in order to concisely refer to specific study areas (Fig 5.1). Visual checks of mooring surface buoys were carried out by boat during the study to ensure receivers were still in position. All receivers were recovered at the end of the study.

A total of 60 sea trout smolts (young sea trout that have begun the smolting process but have not yet reached the marine environment (Thorstad *et al*., 2015)) were tagged with an acoustic transmitter (7.3 x 17mm, weight in air/water of 1.8,/1.1g, 69 kHz, 139 dB re 1mPa at 1 m depth, Thelma Biotel, Trondheim, Norway) implanted in the abdominal cavity of the fish for this study. The minimum fork length of fish tagged in this study was set at 130mm to minimise tagging effects. The tags were programmed to transmit coded acoustic 'pings' every 60 seconds ± 50% (30 – 90 seconds). The minimum estimated tag life for these tags was 80 days. Thirty (30) fish were tagged from the Loch Greshornish catchment and 30 fish were tagged from the Loch Snizort catchment (Fig 5.1).

From the Loch Greshornish catchment, sea trout smolts were caught in the mouth of the Abhainn Choishleadar River (57°28.266′; 006°25.9585′). Of the 30 smolts tagged in this river, 24 were caught in the fyke trap and six were caught using electrofishing equipment on April 23rd in a 20m stretch of river directly upstream of the fyke trap. There is a second river system that flows into Loch Greshornish, the Red Burn (Fig 5.1), but there is an impassable waterfall located at the mouth of the river so it is thought that any trout populations from this catchment would not be anadromous.

Sea trout smolts were primarily captured using fyke net traps located at or near the mouth of a river as it flowed into the sea loch (Fig 5.1). Fish were tagged at the same location where they were trapped (identified in Fig 5.1 as "Tagging Sites"). The fyke traps were kept in position from April 14th to April 23rd until all 60 smolts had been tagged. Anywhere from two to 15 fish were tagged in a day depending on the number of appropriately sized fish caught in the fyke trap. From the Loch Snizort catchment, sea trout smolts were tagged in three rivers. A total of six sea trout smolts were tagged in the River

Haultin (57°28.847′; 006°18.607′). A total of seven sea trout smolts were tagged in the River Tora (57°27.394′; 006°19.423′). A total of 17 sea trout smolts were tagged in two location in the River Snizort (five sea trout tagged at Snizort A (57°26.688′; 006°17.438′) and 12 sea trout tagged at Snizort B (57°26.807′; 006°17.200′)).

To insert the tag, fish were anesthetised using MS-222 and their mass (g) and fork length (mm) were measured. The tags and surgery equipment were sterilized in ethanol before washing with distilled water. The fish were placed on a V-shaped surgery sponge with their ventral side uppermost. A tag was inserted through a ventral incision made to one side of the ventral line. The incision was closed with three interrupted sutures. The fish was then allowed to fully recover (determined by the return of normal behaviour such as holding itself upright without assistance and actively swimming away from stimuli placed in the tank (i.e. a hand inserted into the tank)) in a well oxygenated recovery tank before being released back into the water, downstream of the tagging site.

5.2.1 Data Analysis

Several data filtering techniques were applied to the data to account for suspected fish mortality or dropped tags, as well as false detections caused by tach collisions. To identify possible false detections, the detections of each individual were examined to ensure that no “unusual” movement was occurring. For example, if a Loch Snizort fish was being detected by the estuary and inner arrays within Loch Snizort but was then detected only a few seconds later by a receiver in Loch Greshornish before immediately being detected again by the same inner/estuary receivers, it was determined that the detection in Loch Greshornish was a false detection and removed from the data. Additionally, swimming speed between stations was examined to determine if an individual had been eaten by a larger animal (e.g. seal) that could move at faster speeds than sea trout.

Several metrics of fish movement behaviour were determined from the acoustic telemetry data. These included residency events and rate of movement.

5.2.1.1 Residency events

The amount of time that a detected individual spent within the detection range of a receiver, hereafter referred to as a residency event, was used to determine how much time fish spent in different areas of the array. A residency event was defined as the period from

first detection to last detection in the same detection range of a single receiver, assuming there was no detection at any other receiver and/or no gap in detections exceeding 30 minutes during this period (Honkanen *et al*., 2019).

The mean duration of residency events was calculated for each receiver. This information helped identify fish mortality or dropped tags within range of the receivers. If mortality or a dropped tag was suspected, it would be evident through constant detections of the tag at the same receiver until the final detection of the tag, with no other detections at other receivers or the absence of detections that would have suggested the fish was alive and moved into another area that was not covered by the array.

If the length of time that a tag was constantly detected by a receiver exceeded the mean residency event at the receiver, and if the tag was never detected at another receiver or moved out of detection range for the rest of the study, it was concluded that the fish had expired or the tag was dropped. The detections of that tag were then limited to the same amount of time as the mean residency event at the receiver to account for the fish moving into detection range of the receiver but to also limit any inflation within the dataset that would have occurred if the full residency period of the dead/dropped tag was included in the analysis.

5.2.1.2 Rate of movement

The mean minimum swimming speed of sea trout was estimated as the period of time between subsequent receiver detections during non-residency events. Thus, rate of movement was the distance (by sea) between receivers, divided by the travel time from when a fish was last detected at Receiver A until that fish was first detected by Receiver B.

However, due to the proximity of receivers in some sections of the array, it is not always possible to accurately calculate the swimming speed of sea trout because of an overlap in receiver ranges. With a large detection range, a receiver can report that a fish has reached the location of a receiver when it has, in fact only reached the edge of the receiver's detection range that could still be over 150 m away from the receiver. This can lead to impossibly fast swimming speeds between adjacent receivers.

To account for this effect, receiver lines of the array were divided into “stations” and the swimming speed between stations was calculated (Fig 5.1). Each station comprised receivers in the same small geographic location. For example, the receivers making up a double curtain array were clustered together to form a single station. The receivers comprising each station, as well as receiver ID numbers, can be found in Table 5.1.

5.2.1.3 Calculating home range

The home range of individual fish was calculated using the Minimum Convex Polygon (MCP). This determines the smallest polygon around all points where an animal was located and is a common estimator of home range. However, MCP may sometimes include areas which are not utilised by the individual. To identify more clearly the space used by individuals the MCP level can be set so that ‘outliers’ or positions furthest from the core area of detections are removed. For example, setting the MCP level to ‘60%’ will remove the 40% furthest locations from the core detection area as determined by the mean of the coordinates of the relocations for each animal.

In this study the minimum number of receivers a fish was detected at before a polygon could be determined was set at five. This is due to the proximity of some receivers within the array, and effective detection range of the tags. Using five receivers ensures that fish were actively swimming between receivers instead of being detected within overlapping detection zones.

5.2.1.4 Statistical analysis

Kruskal-Wallis testing was used during analysis to determine if there were statistically significant differences between groups of individuals. Specifically, the method was used to determine if fish length determined an individual’s decision to migrate out of their natal sea loch. This method was chosen based on the non-parametric distribution of the data.

Several statistical models were run using the Loch Greshornish cohort to determine if sea trout post-smolts were being attracted to the net-pen section of the array. A chi squared test was used to examine the frequency of detections of fish at receivers located in the net-pen section of the array relative to the remaining receivers in Loch Greshornish. A GLMM model was used to determine if there was a significant difference in the amount of time individuals spent at the net-pen receivers and the remaining Greshornish receivers.

Table 5.1. List of receivers comprising each station. Locations can be found in Figure 5.1.

Receiver	Station	Location
G1	Station A	Estuary
G2	Station B	Estuary
G3	Station C	Inner
G4		
G5		
G6		
G7	Station D	Middle
G8		
G9		
G10		
G11	Station E	Net-Pen Zone
G12		
G13		
G14	Station F	Outer Line
G15		
G16		
G17		
G18		
S1	Station G	Estuary
S2	Station H	Estuary
S3	Station I	Inner
S4	Station J	Inner
S5		
S6		
S7		
S8	Station K	Inner
S9		
S10	Station L	Middle
S11		
S12		
S13		
S14		
S15		
S16	Station M	Middle
S17		
S18		
S19		
S20	Station N	Outer Line
S21		
S22		

All statistical analysis from this study was conducted in R version 3.6.0 (R Core Team, 2019) using packages VTrack (Campbell *et al*., 2012), sp (Pebesma & Bivand, 2005; Bivand *et al*., 2013), adehabitatHR (Calenge, 2006), data.table (Dowle & Srinivasan, 2019), tibble (Müller & Wickham, 2019), ggplot (Wickham, 2016), lme4 (Bates *et al*., 2015), MASS (Venables & Ripley, 2002), Hmisc (Harrell, 2019) and plyr (Wickham, 2011).

5.2.1.5 Range testing

Tag detection range was tested in Loch Greshornish from March 1st to March 13th, 2017 by deploying six Vemco VR2TX receivers with internal sync tags (power output: 142 dB re 1mPa at 1 m depth) in the middle of the sea loch (Fig 5.1). These receivers were deployed in a line at 50 metres apart with the exception of the final receiver that was positioned 100 metres away from the previous receiver. Maximum detection range was 180 metres.

The detection ranges of two TX receivers (G16 and S21) located on the outer line of each sea loch were monitored throughout the study (April to July 2017) using internal sync tags. The receivers transmitted an acoustic 'ping' every 90 seconds ± 50% (45 – 135 seconds) with a power output equivalent to 142 dB re 1mPa at 1 m depth. Receiver S21 in Loch Snizort showed 90% detection efficiency at 340 metres whilst receiver G16 in Loch Greshornish showed 80% detection efficiency at 310 metres. Given that receivers across the outer lines were deployed on average 300 metres apart, the minimum required detection range would be 150 metres for each individual receiver, thus significant overlaps in detection ranges of receivers were present hence it is unlikely (but possible) a fish may have passed the line undetected. It is expected that receivers closest to the shoreline would have slightly reduced detection efficiencies due to their proximity to rocks which would generate high background noise. For example, Receiver G18 located close to a small rocky island had on average 37% detection efficiency at 280 metres (Fig 5.1).

5.3 Results

The mean fork length of smolts tagged was 157.3 ± 11.1 mm (mean ± standard deviation (SD)). The longest smolt tagged was 183 mm, while the shortest was 138mm. The mean mass of the tagged post-smolts was 40.7 ± 8.5 g (mean ± SD). The largest smolt weighed

61 g, while the smallest weighed 27 g. The Thelma V7 tags used in this study weighed 1.8 g in air. The mean tag burden (% of body weight in air) of the smolt cohort was 4.6 ± 0.9% (mean ± SD), but ranged from 2.9% to 6.7%.

Of the 60 smolts tagged for this study, 46 were detected on the receiver array. There was no significant difference in fork length between those individuals that were detected by the receiver array and those that were not (χ^2= 38.8, df=30, P = 0.1). To accurately reflect the change in life stage from smolt (when the fish was tagged as it migrated through freshwater) to post-smolt (when the fish entered the marine array), tagged fish will hereafter be referred to as post-smolts. Of the 46 detected post-smolts, 20 were tagged in the Loch Snizort catchment (14 from the River Snizort, three from the River Haultin and three from the River Tora) and 26 were tagged in the Loch Greshornish catchment (all from the Abhainn Choishleadar River).

Tagged fish were detected by every receiver in the array, suggesting that sea trout post-smolts utilised the full extent of both sea lochs over the course of the study. The receiver that detected the most individuals was G1with 25 fish detected. Receivers S8 and G15 detected the fewest individuals with only 2 fish detected respectively.

In total, there were 194,435 detections recorded on 40 receivers in the receiver array between 14 April and 28 July. Of this total number of detections, 75,431 detections were reported from the 20 individuals making up the Snizort cohort and 119,004 detections were reported from the 26 individuals making up the Greshornish cohort. The 22 receivers in Loch Snizort reported 75,393 detections and the 18 receivers in Loch Greshornish reported 119,042 detections.

Although all of the fish were tagged over a 10 day period in April, the first detection of each individual on the receiver array demonstrated high temporal variation. The mean number of days that it took for an individual to migrate into the array and be first detected by a receiver was 10.8 ± 13.9 days (mean ± SD). However, this ranged from 0 days to 57 days between tagging and first detection.

The mean number of days that it took for an individual from the Greshornish cohort to migrate into the array and be first detected by a receiver was 11.2 ± 14.2 days (mean ± SD). The mean number of days that it took for an individual from the Snizort cohort to

migrated into the array and be first detected by a receiver was 10.3 ± 13.9 days (mean ± SD).

5.3.1 Survival Over Time

The mean period over which fish were detected from first detection to last detection during this study was 41.5 ± 29.7 days. The longest detection period of an individual fish was 88 days. Of the 46 detected post-smolts, 63% of the tags (29 fish) were still being detected at 30 days, and at 40 days, 21 fish (46%) were still being detected (Fig 5.3). At 60 days after tagging 19 fish (41%) were still being detected and at 80 days, 5 fish (11%) were still being detected on the array. At 90 days, no fish were detected.

The period of detection of a tagged fish (as a response variable) was modelled as a negative binomial distribution on fish length (as an explanatory variable) to investigate the relationship between the two. Fish length did not significantly predict the period over which fish were detected ($P = 0.57$).

Of the 20 detected post-smolts from the Loch Snizort cohort, 55% (11 fish) were still being detected at 30 days, and at 40 days, 8 fish (40%) were still being detected (Fig 5.3). At 60 days after tagging 8 fish (40%) were still being detected and at 80 days, 3 fish (15%) were still being detected by the array.

Of the 26 detected post-smolts from the Loch Greshornish cohort, 69% (18 fish) were still being detected at 30 days, and at 40 days, 13 fish (50%) were still being detected (Fig 5.3). At 60 days after tagging 11 fish (46%) were still being detected and at 80 days, 2 fish (7%) were still being detected by the array.

Fish length did not significantly predict the period over which fish from either the Loch Snizort cohort ($P = 0.90$) or the Loch Greshornish cohort ($P = 0.38$) were detected.

5.3.2 Natal Sea Loch Residency

A total of 33 of the 46 detected fish (71%) were only detected by receivers in their natal sea loch for the duration of the study. Of these 33 individuals, 22 were from the Loch Greshornish cohort and 11 were from the Loch Snizort cohort. Thus, 85% of the Loch

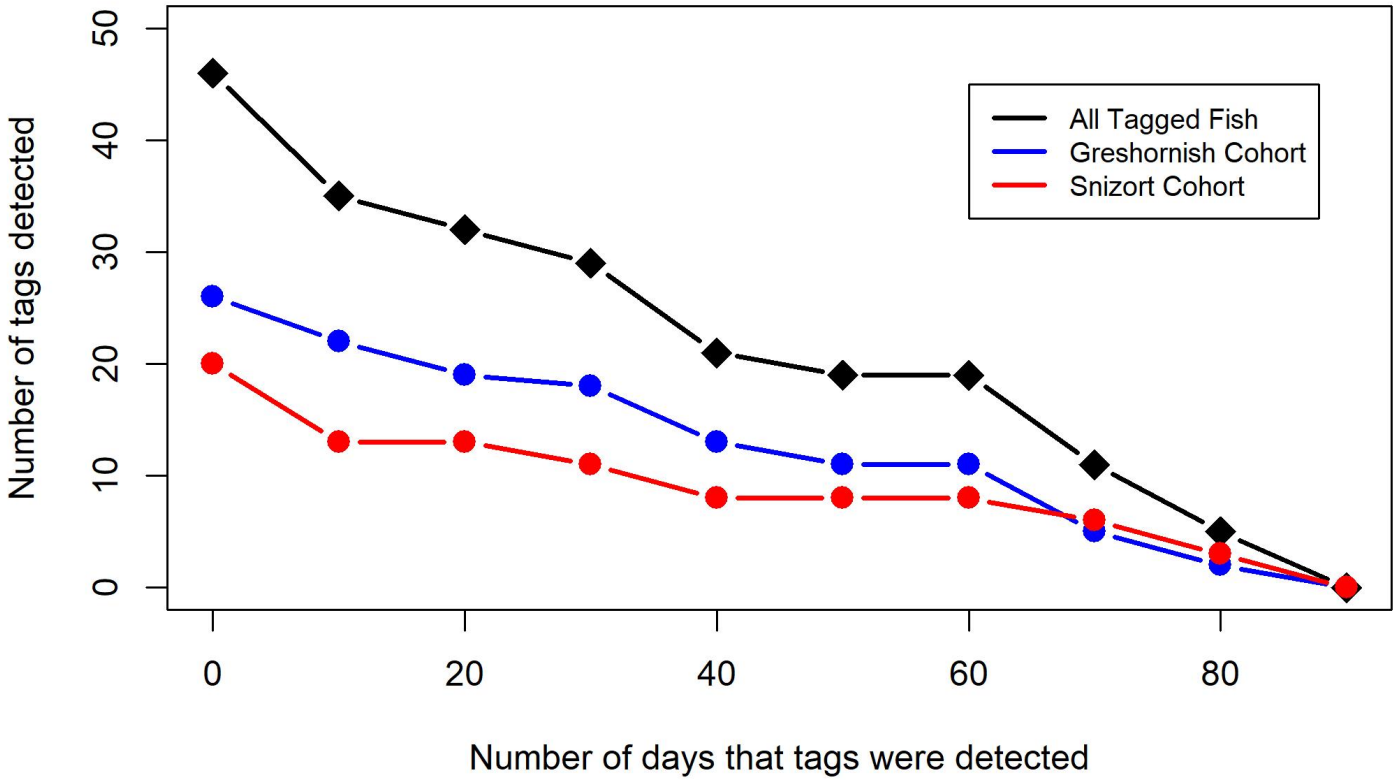


Figure 5.3. The estimated survival of tagged sea trout post-smolts based on the number of days that post-smolts were detected after tagging. The entire population represented by -◆-, while the Snizort cohort is represented by -●-and the Greshornish cohort represented by -●- Some of the observed drop off in detection numbers will be influenced by tag battery life decline later in the study.

Greshornish cohort (22 of 26 fish) and 55% of the Loch Snizort cohort (11 of 20 fish) remained in their respective natal sea lochs for the duration of the study.

Based on daily detection data, most post-smolts spent the majority of their time within the array (Fig 5.4). Some individuals, however, remained undetected for extended periods of time, suggesting they were utilising areas that were either not in range of a receiver or had left the array entirely.

A total of 15 tags were detected by receivers located in the outer lines of the array. Two of these individuals were detected briefly by a single receiver in the outer line but did not appear to leave their natal sea loch as their next detections were reported by receivers in the middle sections of the array suggesting that they migrated back into the middle of the sea loch. The remaining 13 individuals displayed a range of spatial use patterns throughout the rest of the study. These spatial patterns can be broken into three general groups:

(1) Leaving the array

Five of the 46 detected fish (11%) were last detected on the outer lines of the arrays, indicating that they migrated out of the sea lochs and did not return over the course of the study. Two of these individuals were from the Greshornish cohort and three from the Snizort cohort. All five of these fish were last detected by different receivers.

Loch Greshornish

The first individual from the Greshornish cohort to leave the array and not return was last detected on the outer lines on 22 May, while the second individual was last detected on 10 June. The individual that left on 10 June (Tag 97), had previously migrated across to Loch Snizort before migrating out of the array entirely via the outer line of the Loch Snizort array.

Loch Snizort

The first fish of the Snizort cohort to leave the array and not return was last detected on the outer line of the Snizort array few days after tagging on 28 April. The remaining two Snizort individuals were last detected a month apart, one on 25 June and one on 23 July. The individual that left on 23 July (Tag 142), had previously migrated across to Loch Greshornish before migrating out of the array entirely via the outer line of the Loch Greshornish array.

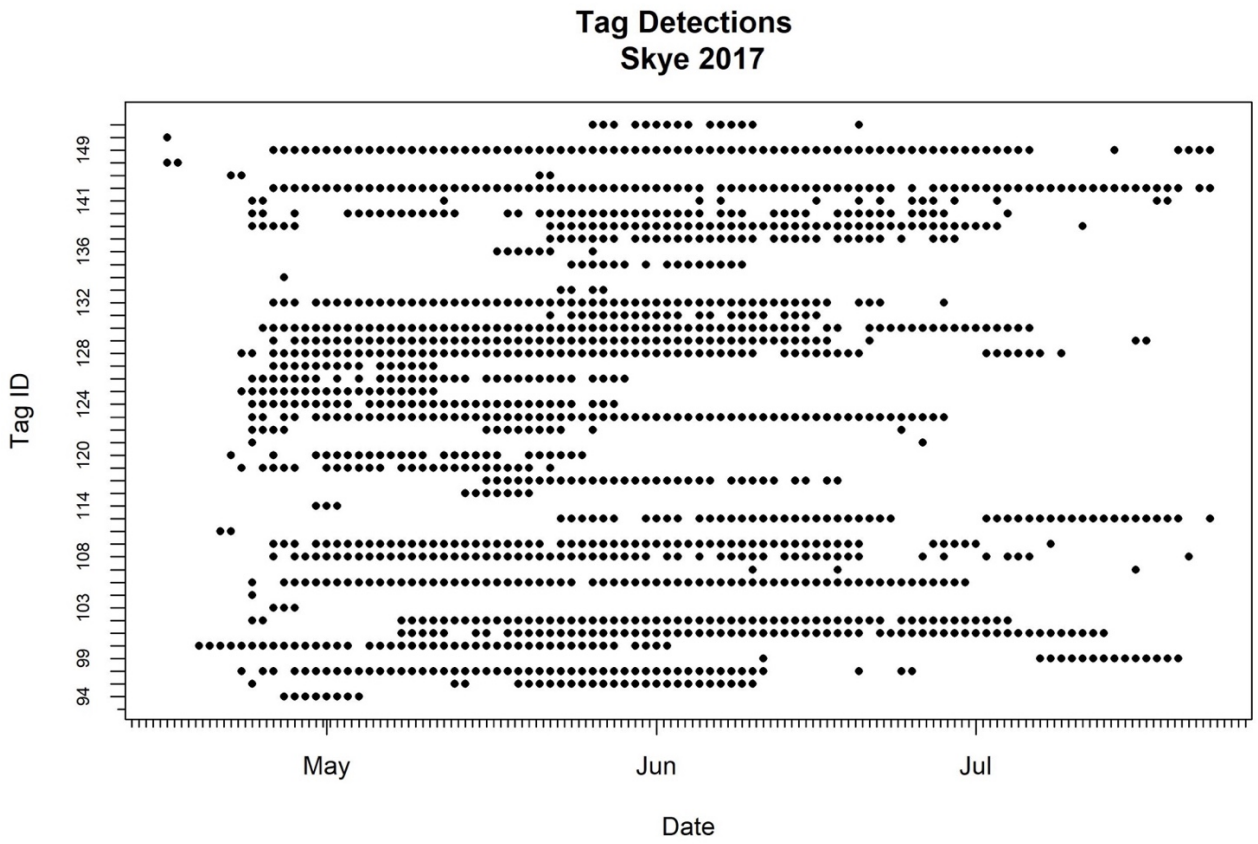


Figure 5.4. A daily presence/absence plot of post-smolt tags. Each dot represents a day (x-axis) that a tag (y-axis) was detected by a receiver in the marine array. If a dot is not present, the tag was not detected on the array.

(2) Exiting and returning to the natal sea loch

Three fish from the Snizort cohort were thought to have migrated fully out of the array only to return back to their natal sea loch system. These three individuals were detected by the receivers in the outer line of the Snizort array and then not detected again for a period of time ranging from an hour to several weeks. When they were detected again, the first detection was recorded at the outer line of the Snizort array, suggesting they were re-entering the sea loch from deeper water. One individual, Tag 129, was not detected for 29 days between exiting and re-entering the Loch Snizort array. This was the maximum amount of time spent outside the array before returning.

All three individuals were thought to have left the sea loch between two and 10 times during the duration of the study, and the mean length of time spent outside the array was 71.6 ± 173.4 hours (mean ± SD; range: 1 – 696 hours).

(3) Migration between adjacent sea lochs

Five of the 46 detected fish (11%) migrated between the two adjacent sea lochs before returning to their natal sea loch by the end of the study, two individuals from Loch Greshornish migrated into Loch Snizort and three individuals from Loch Snizort into Loch Greshornish.

The two Greshornish individuals that migrated to Loch Snizort spent on average 80.5 ± 96.9 hours (mean ± SD) in Loch Snizort before returning to their natal sea loch. The three fish that migrating from Loch Snizort into Loch Greshornish spent on average 46.2 ± 41.9 hours (mean ± SD) in Loch Greshornish before returning to their natal sea loch.

There was no significant difference between the mean length of fish that remained in their natal sea loch for the duration of the study (N= 13) (159.23± 10.2mm) and the mean length of the fish that left their natal sea loch (N= 33) (159.8 ± 9.1mm) (χ^2= 20.1, df=24, P = 0.69).

5.3.3 Spatial Habitat Use Patterns

5.3.3.1 Residency events

A total of 16,998 residency events were reported from the 46 detected individuals over the course of this study. The mean duration of all residency events was 14.8 ± 35.5 minutes (mean ± SD). The receiver with the longest mean residency event was Receiver G2 (in the estuary section of Loch Greshornish) (Fig 5.1). This receiver detected a total of 18 individuals and reported a total of 291 residency events with a mean duration of 66.8 ± 90.3 minutes (mean ± SD). The receiver with the shortest mean residency event was G17 (in the outer line of Loch Greshornish). This receiver detected a total of three individuals and reported a total of eight residency events with a mean duration of 1.2 ± 1.1 minutes (mean ± SD). Only two individuals were responsible for the residency events at G17, the third was only detected once.

Loch Snizort cohort

Detected fish from the Loch Snizort cohort were detected at 34 of the 40 receivers in the full array. A total of 7,360 residency events were reported from the 20 individuals comprising the Loch Snizort cohort. The mean duration of these residency events was 12.4 ± 26.8 minutes (mean ± SD). The receiver that reported the longest mean residency event amongst the Loch Snizort cohort was S17, in the middle section of the sea loch. This receiver detected a total of nine individuals and reported a total of 165 residency events with a mean duration of 42.7 ± 82.7 minutes (mean ± SD). The receiver that reported the overall shortest mean residency event from the Loch Snizort cohort of fish across the entire receiver array was G17 (in the outer line of Loch Greshornish). This receiver detected two individuals and reported a total of eight residency events with a mean duration of 1.2 ± 1.1 minutes (mean ± SD). However, the receiver in the Loch Snizort array that reported the shortest mean residency event from the Snizort cohort of fish was S11 (Located in the middle section of Loch Snizort. This receiver detected eight individuals and reported a total of 31 residency events with a mean duration of 3.2 ± 4.5 minutes (mean ± SD).

Loch Greshornish cohort

Detected fish from the Loch Greshornish cohort were detected at 35 of the 40 receivers in the full array. A total of 9,638 residency events were reported from the 26 individuals comprising the Loch Greshornish cohort. The mean duration of these residency events was 16.8 ± 40.8 minutes (mean ± SD). The receiver that reported the longest mean residency event amongst the Loch Greshornish cohort was the estuary receiver at G2. This receiver detected a total of 18 individuals and reported a total of 291 residency events with a mean

duration of 66.8 ± 90.3 minutes (mean ± SD). The receiver that reported the shortest mean residency event amongst the Loch Greshornish cohort was G15. This receiver detected a single individual and reported one residency event with a duration of 0.4 minutes.

5.3.3.2 Seasonal changes in habitat use

Generally, both populations showed similar increases in home range over the course of the study (Figs 5.5 & 5.6). In April, very few individuals were detected outside the estuary and inner sections of the array. Beginning in May however, there was a gradual increase in the number of post-smolts moving toward the middle lines of the array but fish were still spending the longest periods of time in the estuary and inner sections of the lochs. In June, the post-smolts continued to extend their home range and the highest number of tags were detected in the middle and outer lines than any other time during the study, suggesting that a large proportion of detected individuals were utilising the full extent of the array during this month. By July, the total number of post-smolts detected on the array had declined, but this month reported the widest spatial range of both populations.

April

A total of 73% (19 individuals) of the Greshornish cohort were detected by three receivers in the estuary and inner sections of the Loch Greshornish array in April (Fig 5.5). Only one individual moved beyond G1, the receiver closest to the tagging site. The remaining 18 were only detected at G1. The mean residency time spent at these receivers was 35.0 ± 35.3 minutes (mean ± SD).

A total of 75% (15 individuals) of the Snizort cohort were detected on the Loch Snizort array in April, however the geographic range of these 15 individuals was greater than that demonstrated by the Greshornish cohort (Fig 5.6). The majority of these fish migrated beyond the estuary section of the Loch Snizort array into the inner section during April and were detected on up to nine receivers. The mean residency time spent at receivers in the estuary and inner sections of Loch Snizort was 29.7 ± 23.6 minutes (mean ± SD).
Longer residency events were reported at receivers located in the estuary section and also at receivers located in shallow inlets of the inner section of the array. One single individual migrated out of Loch Snizort during this month and was detected in every receiver section. This was the only individual from either population that was detected beyond the estuary and inner sections of the array during the month of April.

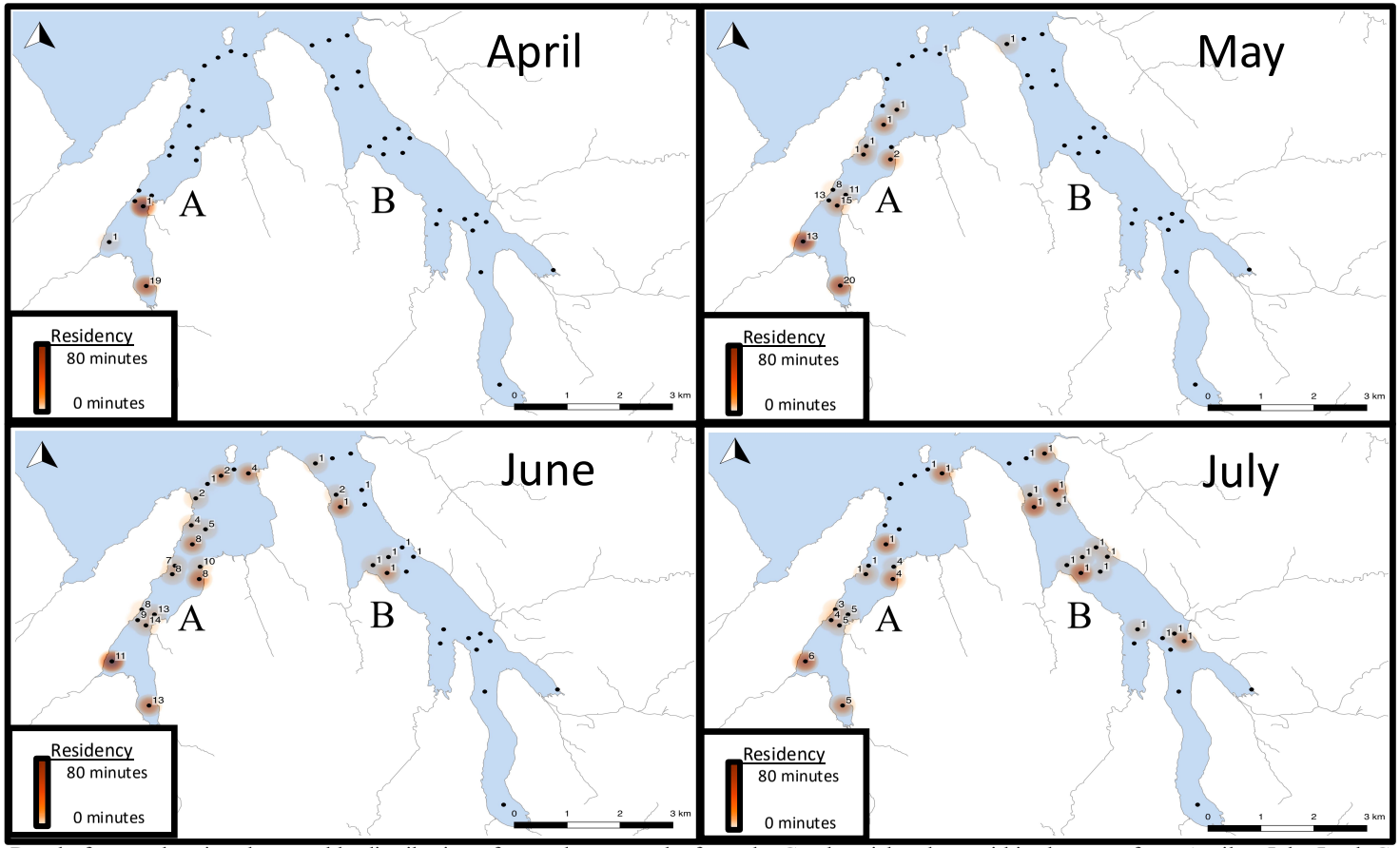


Figure 5.5. Panel of maps showing the monthly distribution of tagged post-smolts from the Greshornish cohort within the array from April to July. Loch Greshornish (left) is identified by "A", while Loch Snizort (right) is identified by "B". Each number next to a receiver represents the number of tags detected by that receiver. In July, only 1 individual post-smolt from the Greshornish cohort was detected in Loch Snizort. The graduated coloured circles represent the mean duration of residency event that post-smolts spent at the receivers. The longest mean monthly residence event reported by a receiver in the post-smolt data subset was 80 minutes.

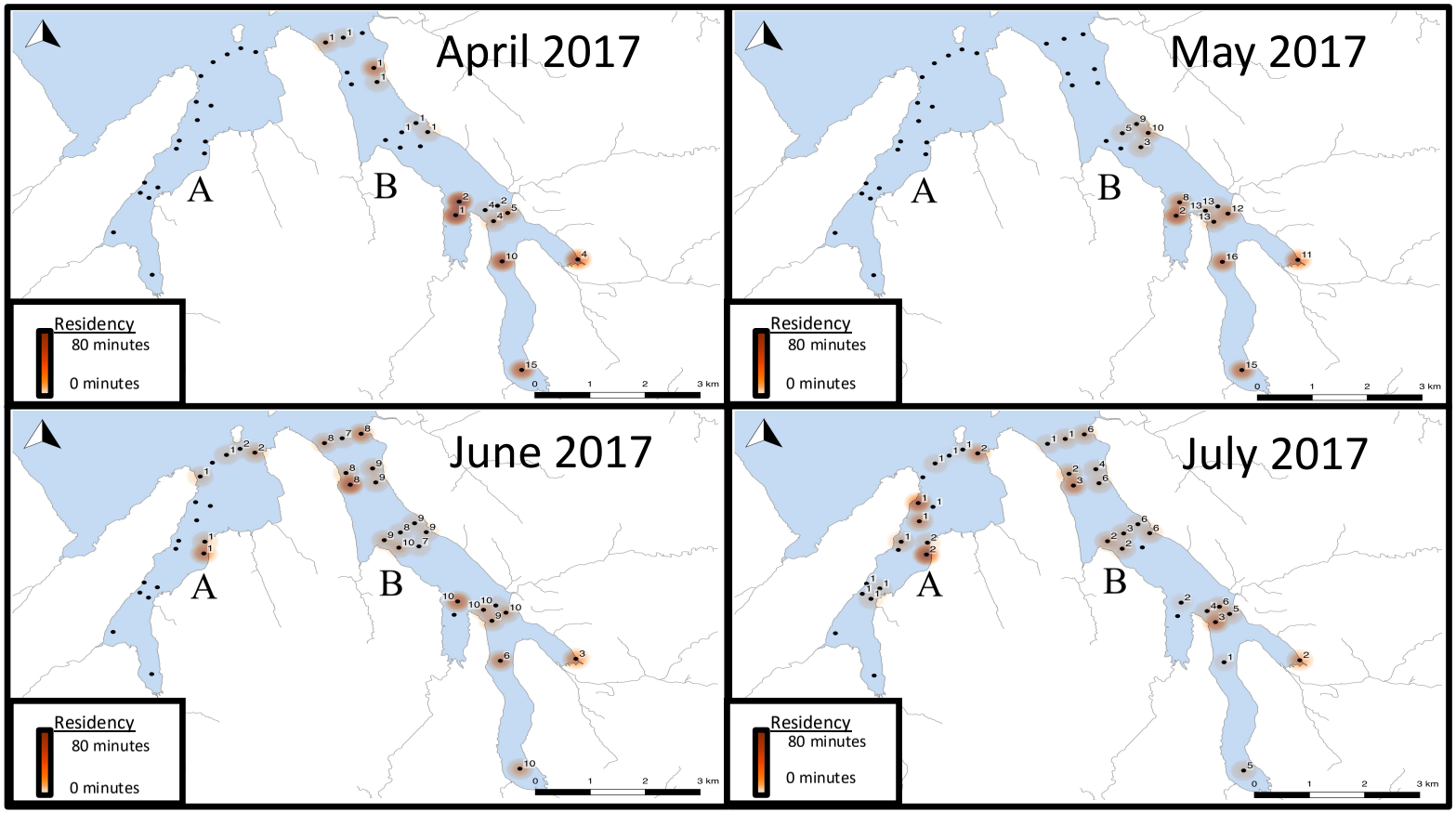


Figure 5.6. Panel of maps showing the monthly distribution of tagged post-smolts from the Snizort cohort within the array from April to July. Loch Greshornish (left) is identified by "A", while Loch Snizort (right) is identified by "B". Each number next to a receiver represents the number of tags detected by that receiver. In July, only 2 post-smolts from the Snizort cohort were detected in Loch Greshornish. The graduated coloured circles represent the mean duration of residency event that post-smolts spent at the receivers. The longest mean monthly residence event reported by a receiver in the post-smolt data subset was 80 minutes.

May

A total of 21 individuals from the Loch Greshornish cohort were detected by 13 receivers in the array in May. Of these 21 individuals, five were detected on the array for the first time. Larger numbers of post-smolts were detected on inner section of the Greshornish array than had been previously. Longer mean residency times were reported from the estuary receivers (55.4 ± 17.6 minutes (mean ± SD)) than in the inner array (5.6 ± 5.5 minutes (mean ± SD)), indicating that detected individuals were spending more time in the estuary than in any other section of the array. Two individuals were detected on the middle section of the Greshornish array and one of these fish continued to migrate out of the array and did not return for the duration of the study. This was the only fish to migrate out of the array during May. The residency events of these two individuals at the middle, net-pen, and outer line were on average 9.3 ± 7.1 minutes (mean ± SD), indicating that the fish were not remaining in these areas for long.

A total of 16 individuals from the Snizort cohort were detected by 13 receivers on the Loch Snizort array in May. Of these 16 fish, four were detected on the array for the first time. The Snizort population showed similar spatial use trends to the Greshornish population during May in terms of an increased number of post-smolts reaching the inner section of the array. However, the Snizort population showed a further increase in home range, with 10 individuals (or 50% of the Snizort cohort) reaching the middle section of the array in May. The receivers in the middle section of the array reported a mean residency event of (6.2 ± 3.3 minutes (mean ± SD). This was considerably shorter than the mean residency events of both the inner section, 18.0 ± 12.4 minutes (mean ± SD), and the estuary receivers, 31.0 ± 3.9 minutes (mean ± SD). These residency events indicated that the Snizort cohort preferred to spend longer periods of time in the estuary and inner sections of the array relative to the rest of the sea loch. The slightly longer mean residency event time reported at the estuary receivers, suggested a preference in habitat, is similar between the two populations of post-smolts, but the difference is more defined within the Greshornish cohort.

June

A total of 17 individuals from the Loch Greshornish cohort were detected by 23 receivers in the array in June. Of these 17 individuals, two were detected on the array for the first time. In June, the largest number of individual tags were active throughout the full extent of the Loch Greshornish array than at any other time during the study. The longest mean residency events were still reported by the receivers located in the estuary of the sea loch

(51.9 ± 36.8 minutes (mean ± SD)), whereas the remaining sections of the Greshornish array reported mean residency events of between 4.8 ± 3.3 minutes (mean ± SD) at the net-pen section and 12.1 ± 8.5 minutes (mean ± SD) at the outer line of the array. This was also the period of time when the first individuals from the Greshornish cohort were detected entering into the Loch Snizort array where they migrated into the middle section of the array. These two individuals were detected on a total of nine receivers on the Loch Snizort array, however, the mean residency events reported at the Snizort receivers was 5.9 ± 7.3 minutes (mean ± SD), indicating they did not spend long within range of these areas.

A total of 11 individuals from the Loch Snizort cohort were detected by 27 receivers in the array in June. Of these 11 fish, one was detected on the array for the first time. Similarly to the Loch Greshornish cohort, this was the period of time when the largest number of individual tags were active throughout the full extent of the Loch Snizort array than at any other time during the study. The receivers located in the estuary section of Loch Snizort continued to report the longest mean residency events time (18.1 ± 8.6 minutes (mean ± SD)), but there was not as great a difference in the length of residency events between sections of the array. For example, the inner, middle and outer sections of the Snizort array all reported overall mean residency events of between 10 and 13 minutes. The one notable exception to this was Receiver S17 that reported a mean residence event of 44 minutes, but this was driven by a single individual. This was also the period of time when the first individuals from the Snizort cohort were detected entering the Loch Greshornish array, a similar cross-over trend demonstrated by the Greshornish cohort during June. Two Snizort post-smolts were detected on a total of six receivers in Greshornish. Although they were both detected at the outer line of the Greshornish array, only one fish was detected further into the sea loch where it migrated to the middle section of the array. The mean residency events of these individuals at the Greshornish receivers was 9.2 ± 8.1 minutes (mean ± SD), indicating that similar periods of time at these receivers as they did at receivers in Loch Snizort.

July

A total of eight individuals from the Loch Greshornish cohort were detected by 29 receivers in the array in July. There were no new tags from the Greshornish cohort detected for the first time during July. The number of tags from the Greshornish cohort that were being detected on the array dropped 50% between June and July. The majority of the tags still being detected were limited to the estuary, inner and middle sections of the Greshornish array, indicating a reduction in the spatial use of the cohort. The receivers in

the estuary section of the Greshornish array reported the longest mean residency event of 31.1 ± 17.3 minutes (mean ± SD), which was longer than the mean residency events reported by other sections of the array. For example, the inner array of Loch Greshornish reported a mean residency event time of 6.9 ± 1.8 minutes (mean ± SD), while the middle section of the array reported a mean residency time event time of 8.3 ± 10.0 minutes (mean ± SD). There was one individual from the Greshornish cohort that was detected on 16 of the 22 Snizort receivers during June, reaching the inner section of the Loch Snizort array before returning to Loch Greshorish by the end of the study. The duration of mean residency events of this individual reported at the inner section of Loch Snizort were of similar length to those times reported in Loch Greshornish, ranging between 6.9 ± 6.7 minutes (mean ± SD). The middle section of the Snizort array reported a mean residency event time of 13.6 ± 13.8 minutes (mean ± SD), demonstrating that the single individual was spending a marginally longer time on average in this area of the loch than elsewhere.

A total of seven individuals from the Loch Snizort cohort were detected by 34 receivers in the array in July. There were no new tags from the Snizort cohort detected for the first time during July. Unlike the Loch Greshornish cohort, the majority of the Snizort individuals continued to use the full extent of Loch Snizort in July and were detected across the estuary, inner, middle and outer sections of the Snizort array. The mean residency event times of each section were 11.4 ± 9.1, 8.0 ± 8.8, 9.8 ± 5.5 and 6.9 ± 3.7 minutes (mean ± SD) respectively, demonstrating that similar amounts of time were being spent by fish in each section of the array. Similarly to the Greshornish population, there were two individuals from the Snizort cohort that were detected on a total of 14 of the 18 receivers in the Greshornish array, indicating that a small number of Snizort fish were utilising a large portion of Loch Greshornish during July. Both of these individuals returned to Loch Snizort before the end of the study. The longest mean residential event time was reported at the middle section of the Loch Greshornish array (23.1 ± 27.7 minutes (mean ± SD)), followed by the net-pen section with a mean residence event time of 17.0 ± 17.2 minutes (mean ± SD).

5.3.3.3 Engagement with net-pens

Three receivers (G11, G12, G13) were deployed around the Greshornish net-pen facility (Fig 5.1). A total of 303 detections from 10 sea trout were recorded by these three receivers, of which nine individuals were from the Greshornish cohort and one individual was from the Snizort cohort. Overall, the mean duration of residency events occurring in

the net-pen section of the array was 22.8 ± 28.6 minutes (mean ± SD) (range: 0.5 -153.9 minutes).

All 10 individual tags were detected at G11 and the receiver recorded 225 detections. There were a total of 37 residency events at G11 with a mean duration of 29.0 ± 38.6 minutes (mean ± SD) (range: 0.5 – 209.5 minutes). A total of 7 individual tags were detected at G12 and the receiver recorded 16 detections. There were a total of two residency events at G12 with a mean duration of 4.7 ± 1.2 minutes (mean ± SD) (range: 3.8 – 5.6 minutes). A total of five individuals were detected at G13 and the receiver recorded 62 detections. There were a total of nine residency events at G13 with a mean duration of 13.4 ± 20.0 minutes (mean ± SD) (range: 0.5 – 63.3 minutes).

Most detections reported in the net-pen section occurred in June, although there were a few fish who were detected near the net-pens in May and July (Fig 5.7). Fish were often detected by the net- pen receivers over several days in June, however, they were frequently detected by other receivers in different stations between their detections at the net-pens, indicating that they were frequently moving between different sections of the array and not simply remaining within detection range of the net-pen section.

A Chi-squared test tested if the frequency of detections of the Greshornish cohort at receivers located in the net-pen section of the array differed from the frequency of detections in the other sections of the Loch Greshornish array. In this study, post-smolts were less likely to be detected at receivers in the net-pen section of the array than would be predicted by the detection frequency elsewhere in Loch Greshornish array. (χ^2= 10.5, df=50, P <0.001).

The mean duration of residency events spent within range of the net-pen receivers as reported by the nine Greshornish individuals was 16.6 ± 19.2 minutes (mean ± SD) and the mean residency events spent at the remaining 15 Greshornish receivers was 14.7 ± 38.8 minutes. A GLMM was used to test for differences in the mean residency periods of fish at the net-pen receivers (Fig 5.1) compared with other receivers in Loch Greshornish; to avoid repeated measures effects, the tag ID of each fish was entered into the model as a random effect. There was no significant difference in the duration of mean residency events at net-pen receivers compared with other receivers in the array (P = 0.09).

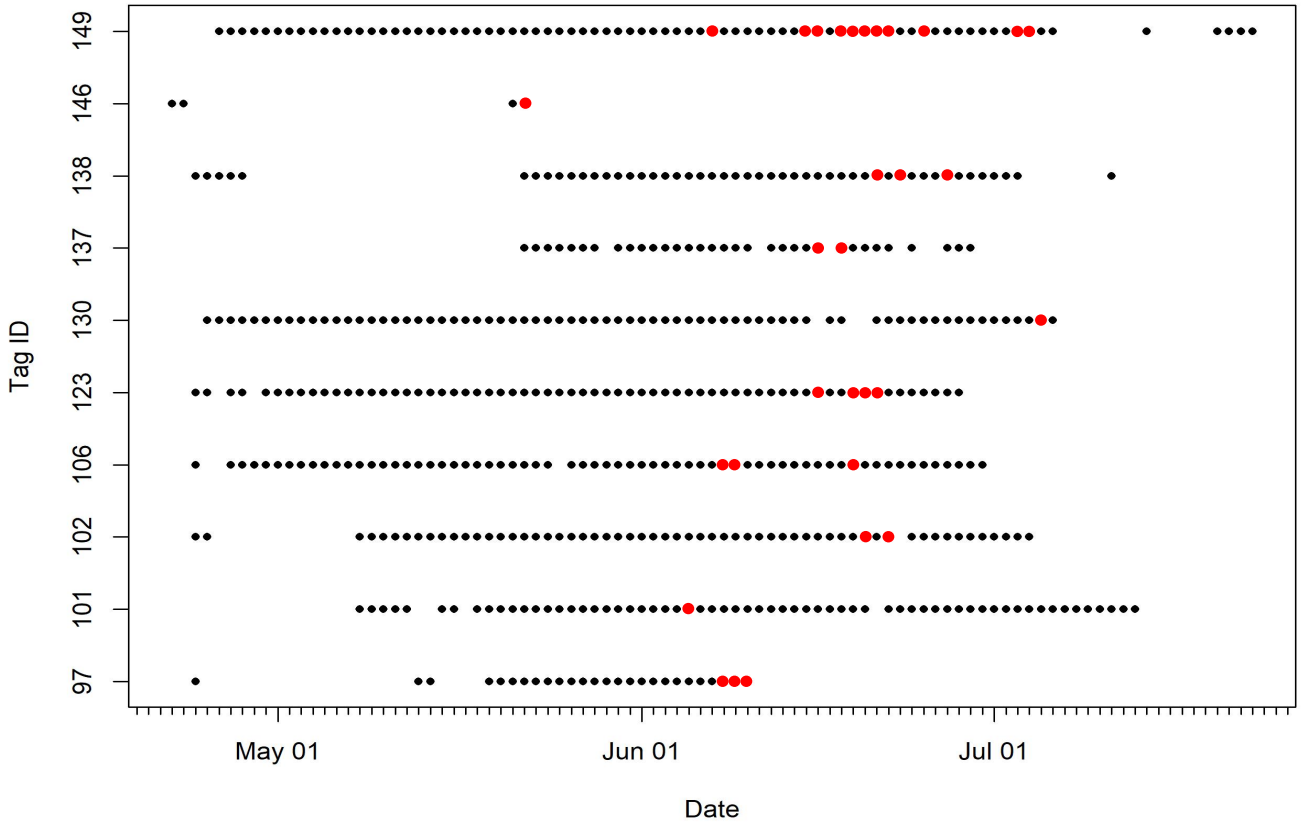


Figure 5.7. A daily presence/absence plot of the 10 post-smolts that were detected at the net-pen section of the array. Each black dot represents a day (x-axis) that a tag (y-axis) was detected by a receiver in the marine array. If a dot is not present, the tag was not detected on the array. Each red dot represents a day that the tag was detected by a receiver in the net-pen section of the array.

5.3.3.4 Possible freshwater re-entry

No receivers were deployed in freshwater rivers so it is not possible to confirm that any individuals swam upstream during the course of the study, but based on the last detections of the fish, it is thought that some individuals could have entered freshwater by the end of the study. Of the Greshornish cohort, seven individuals were last detected at Receiver G1, which is located near the mouth of the Abhainn Choishleadar River (Fig 5.1). The last detections of these seven individuals were spread from May through July. A further seven individuals from the Snizort cohort were last detected on Receiver S1, the estuarine receiver located closest to the mouths of the Rivers Snizort and Tora where these seven fish were tagged in April. The last detections of these fish ranged from May into July, however three of them were last detected at the beginning of July when heavy rainfall increased river height.

Given the proximity of Receiver G1 and S1 to the natal rivers of these individuals and that they were not detected again on the array for the remainder of the study suggests they had left the sea loch and re-entered freshwater before the study had finished.

5.3.3.5 Rate of movement

The mean swimming speed of sea trout was estimated between receiver line stations (Fig 5.1) using non residency events. The overall mean swimming speed of the entire populations of detected fish was 0.33 ± 0.67 m/s (mean ± SD). There was little difference between the mean swimming speeds of the Snizort and Greshornish cohorts, with mean swimming speeds of 0.32 ± 0.59 m/s and 0.35 ± 0.78 m/s respectively.

5.3.3.6 Home range

A total of 29 of the 46 detected sea trout were detected at five or more receivers and thus a home range was calculated, the remaining 17 fish were detected at four receivers or less.

Mean home range measured as an 80% Minimum Convex Polygon (MCP), (that is excluding the 20% of the most distant points of the home range from its centroid) was 315.0 ± 350.9 m^2 (mean $\pm$ S.D.). Tag number 128 had the largest recorded 80% MCP at 1272.1 m^2. This was one of the individuals that migrated between the adjacent sea lochs over the course of the study. At 60% MCP mean home range reduced to 110.2 ± 123.3 m^2.

Despite that all receivers in both study lochs recorded fish, indicating that the whole sea loch was being visited at some point during the study, and that six fish moved between adjacent lochs and that five fish are likely to have migrated out of the study area into more open coastal areas, the relatively small MCP measures of home range indicates that most fish in this study exhibited relatively high site fidelity with fish spending a large proportion of their time in a relatively small area.

A GLM model was developed to investigate the relationship between the size of the 100% MCP occupied by the 29 fish and fish length. Fish length did not significantly predict the size of the area used (P = 0.35).

5.4 Discussion

In this study, 60 sea trout smolts were tagged and 46 were detected on the receiver array, 20 from the Loch Snizort catchment and 26 from the Loch Greshornish catchment. Of the 14 sea trout that were not detected on the array, four individuals were tagged in the River Tora, four were tagged in the Abhainn Choishleadar River, three were tagged in the River Snizort, and three were tagged in the River Haultin (Fig 5.1).

It is thought that if the undetected individuals from the Rivers Abhainn Choishleadar, Tora and Haultin had expired after tagging, the carcasses should have been washed downstream into the estuaries, less than 0.5 km away, where they would most likely have been detected by the receivers located there (Strobel *et al*., 2009; Havn *et al*., 2017). Therefore, it is likely that these fish "de-smolted", a recognised process in salmonid smolts (Jonsson & Jonsson, 2011; Thorstad *et al*., 2012; Gardner *et al*., 2016). Although the exact causes of de-smolting are not fully understood, it is thought that water temperature, stress or lack of access to the marine environment due to barriers could encourage a smolt to change its migratory physiology to remain in freshwater (Jonsson & Jonsson, 2011). There is some evidence to suggest that salmonid smolts that undergo a de-smolting process are capable of re-smolting the following year (Shrimpton *et al*., 2000).

The tagging sites in the River Snizort were located an estimated 3 km upstream from the Loch Snizort estuary and the first receiver (S1, Fig 5.1). Due to this greater distance between tagging locations and the first receiver, it is possible that the four individuals from the River Snizort that were not detected on the array either succumbed to predation during their river migration or expired after tagging but their carcasses remained in the river

where they were not detected. There is some evidence that fish carcasses can be carried in the water column for up to 20 km (Hewson, 1995), which would suggest that there is potential for the expired fish to still come within detection range of a receiver if the river current was strong enough to carry it downstream. But given the suspected de-smolting levels observed in the other three river catchments, it is thought that this small number of individuals from the River Snizort also de-smolted and remained in freshwater.

There was considerable temporal variation in the time it took for smolts to migrate into the marine array. A total 75% of the post-smolts had been detected on the receiver array by May 1st, indicating that they had moved far enough into the marine environment to be detected by the receivers located in the estuaries closest to their natal rivers. This coincided with a slight increase in river height around April 24th due to increased rainfall. Increased rainfall can often initiate post-smolt migration (Jonsson & Jonsson, 2011). The remaining fish took anywhere from 21 to 57 days to be detected. However, this prolonged migration period is common amongst brown trout populations, particularly in colder environments (Jonsson & Jonsson, 2011; Thorstad *et al*., 2016).

Based on the reported detection levels, there was a 25% decline in sea trout post-smolts in the array within the first 10 days after their initial detection in the marine array. The first weeks in the marine environment are crucial to sea trout post-smolt survival and with unfamiliar pressures like predation and adjustment to saline conditions, high mortality rates amongst post-smolt are suspected (Thorstad *et al*., 2016). Middlemas *et al*. (2009) reported a 50% loss in the number of fish detected in the first two weeks of their study, suggesting a slightly larger decline to that reported here. Although some of this decline in the detected population could represent mortality, several tags were detected multiple times over the following weeks, indicating that some of the individuals must have migrated to a location outside the receiver range before returning to the array. It is reasonable that the site fidelity exhibited within the array receivers, particularly towards receivers in estuarine areas such as Receivers S1, S2, G1 and G2, was shown in other locations outwith the detection area of acoustic receivers.

5.4.1 Coastal Zone Use

One aim of this study was to examine if sea trout post-smolts remain within their sea loch of origin during their first summer at sea or if they migrate out into the wider coastal marine environment. The decline in detection levels continued over the summer, likely influenced

by mortality and decreasing battery life of the tags, however, it is apparent that sea trout post-smolts spent large amounts of their time foraging in the sea lochs, particularly in estuarine areas during April and May, instead of moving out to the deeper water of the ocean or returning to freshwater. This would suggest that there was some benefit to remaining in these areas, either a better food supply or shelter from predators. Of the 46 detected post-smolts, only 11% were detected leaving the array through the outer line without returning during the study. Of those fish that remained active in the sea loch, longer residency events were initially recorded in estuarine areas and along the coastline than in deeper and more open water of the sea loch.

These patterns of habitat use are similar to those demonstrated in the few other studies of sea trout marine habitat use in Scotland. Sea trout have been documented remaining near to their natal river several weeks after their initial migration into the marine environment (Pemberton, 1976; Middlemas *et al*., 2009). Coastal areas are also well documented as habitats used frequently by sea trout, particularly in the first months of their marine migration (Davidsen *et al*., 2014; Thorstad *et al*., 2016).

However, this is the first study of its kind that has followed the migration of Scottish sea trout beyond their natal sea loch. While the majority of sea trout post-smolts in this study remained in their natal sea loch for the duration of their first summer in the marine environment, a small percentage of sea trout did migrate around the coastline and into other sea lochs, highlighting the importance of coastal zones beyond the natal sea loch for the post-smolt life stage. Eight individuals, or 17% of the detected sea trout post-smolts, migrated out of their natal sea loch only to return later to that same sea loch before the conclusion of the study. Five of these individuals migrated into the adjacent sea loch (either Loch Greshornish or Loch Snizort) where their movements could still be tracked and remained there for anywhere between a few hours up to several days before returning to their natal sea loch. Additionally, three more individuals migrated out of the array and were not detected for varied periods of time (several hours to weeks) when they might have migrated out into deeper water or along the coastline beyond the receiver array before returning to their natal sea loch. Some studies have found that larger post-smolts are more likely to migrate into deeper water (Flaten *et al*., 2016), however, this study showed that body length was not a significant driver behind longer migration distances, a similar result to del Villar-Guerra (2014).

5.4.2 Engagement with Net-Pens

A second aim of this study was to determine if sea trout smolts are attracted to net-pen aquaculture facilities. Research has demonstrated that fish, particularly in warmer climates such as Greece (Machias *et al*., 2006) and Brazil (Demétrio *et al*., 2011), can be attracted to aquaculture facilities (Uglem *et al*., 2014). Attraction to net-pens can be driven by the availability of excess food falling through the openings of the net-pens or the physical structures of the pens providing habitat and shelter for wild fish (Callier *et al*., 2018). Fish can also be deterred from approaching these structures by the noise and disturbance caused by various maintenance and feeding mechanics, as well as environmental pollution from the pens (Callier *et al*., 2018). Studies regarding the wild salmonid-specific interactions with net-pens has not been researched as thoroughly (Thorstad *et al*., 2012).

From this study, an estimated 21% of the detected sea trout (i.e. 10 individuals) came within detection range of the receivers located at the net-pens. When comparing the overall mean residency events that occurred at the pens and at receivers elsewhere in the array, there is little difference in the duration of the residency events. This indicates that in general the 10 individuals that were detected near the pens are not spending longer periods of time within the detection range of the pens relative to the amount of time they spend elsewhere in the array. Furthermore, only 48 residency events were recorded by the receivers located by the net-pens. The majority of the 10 individuals reported less than seven residency events at these receivers with the exception of Tag 149, which reported 24. This would suggest that these 10 individuals, except perhaps Tag 149, were not actively drawn to the net-pens as a location of increased resources or protection.

5.4.3 Temporal Changes in Spatial Use

The third aim of this study investigated the changes in coastal habitat use patterns of sea trout post-smolts over the summer months of their maiden sea migration. Post-smolts from this study showed a gradual increase in home range size as the summer progressed (Figs 5.5 & 5.6), a similar finding to Middlemas *et al.* (2009). During April and May, the detected fish remained primarily in the estuary, inner, and middle arrays of both sea lochs. The near-shore habitat preference of sea trout post-smolts is well documented (Flaten *et al*., 2016; Thorstad *et al*., 2016). As the summer progressed, more fish were detected on receivers by receivers further out in the array (Figs 5.5 & 5.6), suggesting that as some post-smolts continued to feed, they would gradually expand their home range and feeding grounds. Although there is an increase in the spatial distribution of detected fish as the

study progressed, higher numbers of tags were generally detected on the estuary, inner and middle sections of the array, suggesting that not all fish were migrating through the full extent of the array or out into deeper water.

Similar results were reported by del Villar-Guerra *et al*., (2014) and Ferguson *et al*. (2019b), demonstrating that while some fish migrate into deep water ("anadromous" fish), other individuals from the same population will remain in more estuarine areas ("semi-anadromous" fish). The study presented here has reported a similar intrapopulation variation of the habitat preference of individual post-smolts, but with a majority of the population demonstrating "semi-anadromous" tendencies.

Loch Greshornish is an estimated 6 km in length and Loch Snizort is an estimated 9 km in length. The middle sections of the array were roughly located between 4 km (Loch Greshornish) and 7 km (Loch Snizort) (distance measured by sea) from the natal rivers of the detected fish. Therefore, the majority of post-smolts in this study remained within 4 -7 km of their natal river during their first summer in the marine environment. This is a similar result to that of Middlemas *et al.* (2009) who reported that 37 % of sea trout post-smolts were detected more than 6 km from their natal river, while the remaining majority of fish migrated less than 6 km.

5.4.4 Differences Between Populations

The final aim of this study was to determine if populations of different catchments act similarly in their use of coastal habitats. Kallio-Nyberg *et al*. (2002) and Middlemas *et al*. (2009) reported that different populations of sea trout originating from different rivers can disperse in different ways. Over the course of this study, both the Greshornish and Snizort cohorts both gradually increased their home range but the majority remained in their natal sea loch. Beyond this behaviour, there were two differences in habitat use between the two cohorts of fish.

Firstly, 45% of post-smolts from the Loch Snizort cohort (nine of 20 detected fish) were found to migrate out of their natal sea loch (six returned), while only 15% of the Loch Greshornish population (four of 26 detected fish) were found to have migrated out of the array (two returned). Although the mechanisms driving the Loch Snizort population to migrate out of their natal sea loch are not fully understood, it is suspected that this behaviour could be driven by resource availability. del Villar-Guerra *et al.* (2014)

hypothesised that the migratory range of sea trout post-smolts is related to several characteristics of the coastal habitat that the fish enter upon leaving their natal river, such as resource availability and low water exchange. After assessing the accessible benefits in the immediate fjord or sea loch system, an individual will then decide to remain or to migrate further. There is little information available on the seabed geography of both sea lochs, however, Loch Greshornish is slightly shallower than Loch Snizort, indicating that it could provide a more productive environment for marine life and thus more available food resources for foraging post-smolts. Therefore, it could be suggested that Loch Greshornish was able to meet the resource demands of their post-smolt population, resulting in a larger proportion of individuals remaining in their natal sea loch for the duration of the study.

Secondly, the habitat use of both populations varied slightly in the month of July. In Loch Greshornish, the majority of detected individuals began to cluster around estuary, inner, and middle sections of the receiver array by the end of the study, with the exception of one individual that continued to migrate between lochs in July. Based on the duration of mean residency events during July, the Loch Greshornish population showed a preference for the estuary section of the array. A similar decline in the spatial range used by post-smolt populations later in the summer was also observed in another telemetry study carried out in a similar sea loch habitat on the west coast of Scotland (Moore *et al*., 2020).

The Snizort cohort, however, was found to still use the full extent of Loch Snizort and the duration of mean residency events became more evenly dispersed across the different sections of the array suggesting that this cohort of post-smolts were no longer demonstrating a preference for the estuary section of the sea loch. The continued use of the entire sea loch by the Snizort cohort could be driven by the availability of resources, but this is speculative.

From these results, the study has demonstrated that there is both intra- and interpopulation variation in the spatio-temporal distribution of sea trout post-smolts over time. Several studies have identified drivers of sea trout migration ranges, including pre-migration physical condition (Eldøy *et al.,* 2015; Bordeleau *et al*., 2018), sex bias (Birnie-Gauvin *et al*., 2019), behavioural and genetic traits (Eldøy *et al*., 2019) and available resources in the marine environment (del Villar-Guerra *et al.,* 2014; Quéméré *et al.*, 2016). This study was not designed in a way that allowed us to evaluate these individual drivers in depth, but they could play a role in the migration continuum of sea trout post-smolts observed here.

5.4.5 Influence of salmon lice on movement

Sixteen (16) individuals that entered the receiver array were last detected by the receiver closest to their natal river, which could suggest that they re-entered freshwater before the completion of the study. These 16 sea trout post-smolts remained in the marine environment for time periods ranging anywhere from a few weeks to three months before their last detections. This could be a demonstration of strong fidelity to the natal river, a well-known behaviour of salmonids, but also could suggest that fish are returning to freshwater after only a short period of time in the marine environment. Although it is not unusual for sexually immature fish to return to freshwater to overwinter (Jonsson & Jonsson, 2009a; Thorstad *et al*., 2016), this potential upstream migration is earlier than was expected.

One potential driving factor that could be contributing to this early freshwater re-entry is the level of salmon lice infestations on the wild sea trout post-smolts. Research has demonstrated that re-entry into freshwater prior to spawning is a common "de-lousing" behavioural response of sea trout when they are infected with high levels of salmon lice (Gjelland *et al*., 2014; Shephard *et al*., 2016; Halttunen *et al*., 2017). Thorstad *et al.* (2015) reported that since the 1990's, several countries have observed early freshwater returns of heavily infested sea trout post-smolts that can occur after only a few weeks at sea. This extended stay in freshwater can result in reduced growth opportunities and fecundity due to reduced resources, as well as secondary bacterial or fungal infections arising from the physical damage incurred from high salmon lice infestations (Thorstad *et al*., 2015).

Based on routine salmon lice counts collected by a local fisheries organization in Loch Greshornish in July 2017, the mean number of salmon lice on the wild sea trout population collected from the marine environment was 30.0 ± 34.2 lice (mean ± SD) per individual, ranging from zero (0) lice to 131 lice (Moore, 2017, unpublished data). This meant that the salmon lice load on sea trout in this area exceeded the normal parasite levels (4-8 lice per fish) that is expected in areas without net-pen Atlantic salmon aquaculture (Thorstad *et al*., 2015). A large proportion of the sampled salmon lice population was made up of juveniles (i.e. chalimus and copepodid life stages), however, some adult mobile life stages were also present. The mean mass (g) of the sea trout sampled in this unpublished study in July was 121.8 ± 88.8 g, giving this population a mean salmon lice density of 0.25 lice g^{-1}. Based on

a classification system proposed by Taranger *et al*. (2015), this salmon lice burden could result in an additional 50% extra mortality for sea trout.

Net- pen aquaculture can lead to increased levels of salmon lice in the water column up to 30 km away from the pens (Middlemas *et al*., 2013). Furthermore, it has been demonstrated that the highest salmon lice burdens on wild sea trout can occur between 7-13 km away from the nearest net-pen facility (Gillibrand & Willis, 2007; Moore *et al*., 2018). Therefore, it was thought that the sea trout in both Loch Greshornish and Loch Snizort were exposed to high salmon lice burdens during the summer months of 2017, thus potentially influencing their decision to re-enter freshwater prematurely.

The results of this study add to research demonstrating that it is not only fish that come into direct contact with aquaculture facilities that are potentially changing their migration techniques to counteract the negative impacts of salmon lice.

In conclusion, this study demonstrated that sea trout post-smolts have a strong preference for estuarine feeding grounds in the first few months of their marine migration. As they grow larger, the fish are able to utilize habitats in deeper waters, but the majority prefer to remain in their natal sea loch system. A small percentage of sea trout migrate beyond their natal sea loch to forage in adjacent coastal areas, but seem to maintain a strong fidelity to their natal system and often return after brief excursions. These results demonstrate that sea lochs are critically important habitats for sea trout populations and therefore should be prioritised as conservation areas in future management plans of Scottish sea trout.

Limited contact is made between wild sea trout and the net-pens used in salmon aquaculture. But given the possible freshwater re-entry behaviour observed in this study and evidence of increased salmon lice abundance reported in Moore *et al*., 2018, it is probable that the presence of net-pens and the resulting increase in salmon lice densities are affecting sea trout populations in nearby sea lochs as well as the habitat where the pens are located.

Given the importance of Scottish sea lochs to young post-smolt and the negative influence of net-pen Atlantic salmon aquaculture on them, the potential future impacts of the increasing aquaculture industry on sea trout populations could be substantial.

6. General Discussion

The brown trout (*Salmo trutta* L. 1758) is widespread across much of the world (Jonsson & Jonsson, 2011). The freshwater life stages are well researched, but less is known about those individuals implementing an anadromous life history strategy (i.e. sea trout). Despite the understanding that sea trout use similar marine habitats as the better understood Atlantic salmon (*Salmo salar* L. 1758) and are thought to face similar threats, sea trout often do not receive the same level of public interest or research funding as their salmonid cousin (Mills, 1989; Harris & Milner, 2006; ICES, 2016; ICES, 2017). However, sea trout populations continue to support both commercial and recreational fishing economies (Harris & Milner, 2006; ICES, 2017), indicating that more attention should be given to this remarkable polytypic species.

Because of the tendency to overlook sea trout, there is limited long term data available which makes it difficult to provide an accurate picture of historical population trends. This has resulted in trout being listed as a species of Least Concern by the Global ICUN Red List (Wilson & Veneranta, 2019). However, from patchy data that are available from countries such as Norway and England, it appears that sea trout populations are behaving differently across a wide spatial range, with some populations demonstrating numerical declines, while others show increases (Davidson *et al*., 2017; Evans & Harris, 2017; Höjesjö *et al*., 2017). The literature suggests that several factors could be driving the observed declines, such as overfishing, climate change, declines in available prey items and anthropogenic developments in important habitats (ICES, 2016).

Historically, Scotland has supported robust sea trout populations in addition to large Atlantic salmon populations (Campbell, 1971; Mills, 1989). Based on raw catch data (Marine Scotland, 2019), it is evident that both species have suffered declines across Scotland since the 1970's, but while extensive research has been directed to better understanding the loss of Atlantic salmon in both freshwater and marine environments, less attention has been given to sea trout populations and the drivers behind their decline.

Previous research has suggested several potential drivers of sea trout population decline in Scotland. These include overfishing (Hastie & Cosgrove, 2001), acidification from human

industrialisation and extensive conifer plantations (Moore *et al*., 2017; Prodöhl *et al*., 2019), predation by birds and marine mammals (Harris *et al*., 2008) and a loss in prey items such as sandeels (*Ammodytes marinus*) (MacDonald *et al*., 2019). More controversially, the potentially negative influences of Atlantic salmon aquaculture have been highlighted as a further driver of population change on the west coast of the country (ICES, 2013; Shepherd *et al*., 2016).

One major goal of the work of this thesis was to determine drivers of long term population changes of sea trout across Scotland. Of the suspected stressors of Scottish sea trout populations, many have been present for decades, but given continuous anthropogenic encroachment and increasing demands on the natural environment, it is highly plausible that the magnitude of their impact has changed over time.

An example of this increasing pressure is the continued expansion of the marine based Atlantic salmon aquaculture industry in Scotland. Salmon aquaculture occurs on the west and north coasts of Scotland in sheltered sea lochs that are also important habitats for a plethora of marine wildlife, such as sea trout (Shephard *et al*., 2016; Moore *et al*., 2018). As outlined in the General Introduction of this thesis (Chapter 1, Fig 1.2), Scotland's salmon aquaculture industry increased by 91% from 1997 to 2017 and future projections demonstrate that the industry will continue to grow in the coming years (Munro, 2019).

The expansion of the salmon aquaculture industry has been associated with increased levels of pathogens and disease in the water column which are then transferred to other organisms in the surrounding area (Thorstad & Finstad, 2018; Skarðhamar *et al*., 2019). One of the most widely recognised pathogens is the ectoparasite *Lepeophtheirus salmonis*, the salmon louse, which is known to cause severe physical damage to sea trout that have high lice burdens (Thorstad *et al*., 2015). Several studies have demonstrated that salmon lice populations can be carried from their point of origin by tidal and wind driven currents for up to 30 km (Middlemas *et al*., 2013), increasing the level of exposure to sea trout not only occupying the same coastal habitat as aquaculture facilities, but also to sea trout populations further afield where an aquaculture a facility might not be in the immediate vicinity (Rabe *et al*., 2020). A significant portion of the work in this thesis focused on the possible impacts of salmon aquaculture on Scottish sea trout populations.

In addition to the recognized negative effects of salmon aquaculture, there is also some evidence that suggests these effects could worsen with increasing climate change driven pressures (Collins *et al*., 2020; Crosbie *et al*., 2020). For example, salmon lice are capable of reproducing more quickly in warmer temperatures (Hamre *et al*., 2019) and increased lice densities have been reported on sea trout in years that are warmer and drier (Shephard *et al*., 2016) indicating that as sea temperatures rise and more extreme weather events, such as prolonged droughts, occur, sea trout populations may be under increasing threat from the expansion of aquaculture around the coastline of Scotland.

Thus, this thesis comprised four separate, but linked studies investigating long term Scottish sea trout population trends in changing marine environments.

Firstly, I used a historic timeseries of Scottish sea trout catch data to address a number of questions around the temporal and spatial patterns of population change and to examine the putative drivers of that change. Using a Theoretic Information modelling approach, I was able to successfully identify consistent drivers of change behind the population trends of Scottish sea trout over the last seven decades. From the results, sea trout populations saw an overall decline of 48% since 1952, but there was great spatial variation in the rate of decline. Populations in catchments draining to the west coast of Scotland declined at a faster rate than east coast populations, with some rivers located on the east coast actually reporting increases in their sea trout populations over this time period. The most consistent driver of change in sea trout populations was river length, with longer rivers generally supporting larger populations, although this effect varied regionally. Although the effect of river length was largely different between regions at the beginning of the dataset, the strength of the effect declined over time until sea trout populations, regardless of river length, were reacting similarly across Scotland by the end of the time series. This result suggests that historically resilient populations (i.e. populations from longer rivers) were become less resilient with time. Other consistent drivers of population change were winter rainfall, mean river gradient, and the percentages of calcareous, peatland and solid bedrock geology. Several of these variables reported increasingly complex relationships with other drivers over the course of the data series, indicating that the strength of their effect changed over time.

This work provides new information on the population trends of Scottish sea trout where there had been no previous quantitative assessment. While a few rivers in Scotland have

shown increases in their sea trout populations, the overall decline of sea trout across the country would indicate that populations have suffered a large decline in recent decades. Therefore, one conclusion of the work presented here is that their IUCN status as a species of Least Concern should be reconsidered. By identifying the drivers that have influenced sea trout populations previously, there is the opportunity for management policies to be developed that use the results of this study to predict how populations will be impacted in the future. Additionally, now that these historically important drivers have been identified, future analysis can incorporate them and other variables such as alterations in land use, other fishing methods, predation and trends in Scottish Atlantic salmon populations into more advanced models to account for further changes in sea trout population trends.

Secondly, I used an abbreviated subset of the long term data series to address the impacts of Atlantic salmon aquaculture on a specific geographic range of sea trout populations on the west coast of Scotland. The aims of this study were to determine if the presence of aquaculture facilities influenced the population size of sea trout on the west coast of Scotland and, where facilities were present, what impact, if any, the annual biomass produced at a facility had on sea trout population size. As with the previous chapter, I used an Information Theoretic modelling approach to identify a series of environmental, climatic and aquaculture related variables that could be acting as important drivers of west coast sea trout populations over the last two decades. Sea trout populations size was found to be acting differently in rivers with and without aquaculture facilities within 30 km. Furthermore, in rivers where aquaculture facilities were present nearby, an increasing annual biomass of facilities had an increasingly negative effect on sea trout populations. These relationships were often relatively complex and linked with climatic variables, such as winter rainfall and sea temperature, and invariant catchment characteristics, such as river length. The effects of increasing biomass on sea trout populations size were also shown to be worsened during periods of low winter rainfall and high annual sea temperatures.

This work provides the first quantitative assessment of the long term effects of the Scottish salmon aquaculture industry on local sea trout populations sizes on the west coast of Scotland. Although there is an increasing body of evidence that demonstrates the negative impacts of aquaculture on Scottish sea trout, which is supported by the results of this chapter, the study also identified several climatic variables that may magnify the effects of aquaculture. These results suggest that the effects of aquaculture will continue to worsen as

the industry grows and as projected climate change pressures increase. Future analysis could provide further information about the direct impacts of aquaculture on sea trout by incorporating biomass data from as early as the 1970's when the industry began to expand quickly, as well as including additionally ecologically relevant data such as salmon lice counts from aquaculture facilities, the introduction of various treatment methods such as biocides and cleaner fish and the stage in the production cycle of aquaculture facilities within 30 km of the rivers.

Thirdly, I investigated the distribution of salmon lice burdens on wild sea trout relative to their proximity to the nearest salmon aquaculture facility. The aims of the study were to determine how salmon lice burdens and life stage specific distributions varied on sea trout in five different locations on the Isle of Skye, Scotland with varying distances from the nearest aquaculture facility. This data was analysed using a hurdle model process to determine the likelihood of a sea trout being infected with salmon lice given their proximity to the nearest aquaculture facility and how, on sea trout infected with the parasite, salmon lice burdens and age structures changed relative to facility proximity. From the results, salmon lice burdens were negatively correlated with distance to aquaculture facilities, meaning that higher lice burdens were found on those sea trout sampled at a shorter distance from aquaculture facilities. Furthermore, the salmon lice burdens of sea trout sampled within a short distance from aquaculture facilities were comprised of predominantly juvenile lice life stages. This indicated that the aquaculture facilities are potentially operating as source points for increased salmon lice populations.

This work adds to growing evidence of the negative impacts of Scottish salmon aquaculture by demonstrating that higher levels of salmon lice originating from aquaculture facilities are impacting sea trout that are foraging in locations up to 13 km away from the facility. As the aquaculture industry continues to expand and more facilities are developed around the coastline, salmon lice levels can be expected to increase in the immediate vicinity of these areas, but have the potential to distributed further afield where additional sea trout populations can be negatively impacted. Future studies might include modelling the empirically measured lice burdens on sea trout using actual salmon lice counts from the nearby aquaculture facilities.

Finally, in order to gain a better understanding of the marine movements of sea trout post-smolts, I used acoustic telemetry methods to tag 60 post-smolts in two adjacent sea lochs on the Isle of Skye, Scotland. The aims of this study were to determine the spatial habitat use of sea trout post-smolts in coastal zones during their first migration into the marine environment, to identify any differences in spatial and temporal habitat use between populations and to determine if the fish were attracted to an aquaculture facility located in one of the sea lochs. From the results, the majority of the detected post-smolts remained in their natal loch over the course of the study or returned to the same loch after short distance migrations into adjacent sea lochs, demonstrating a high level of fidelity to their natal sea loch. Additionally, a small percentage of the tagged fish were detected near the aquaculture facility in the sea loch, but did not spend a significantly longer period of time in the area relative to the rest of the sea loch, suggesting that post-smolts are not actively attracted to aquaculture facilities.

This work provides a closer look at the habitat use of Scottish sea trout post-smolts in the marine environment, a part of the life cycle that is still not well understood. The behaviour of the detected individuals demonstrates the importance of coastal sea lochs to vulnerable sea trout post-smolts during their first summer at sea. Although it is interesting to discover that sea trout post-smolts are not actively spending more time in close proximity to aquaculture facilities, it is clear from the results of Chapter 4 that salmon lice levels can be higher in areas up to 13 km away from a facility, suggesting that sea trout post-smolts using sea lochs adjacent to aquaculture sites could be at greater risk of acquiring unnaturally increased levels of sea lice. Future telemetry studies of Scottish sea trout could investigate if the strong fidelity to natal sea lochs remains with sea trout as they age or if they are more likely to migrate further as they grow before returning to their natal river to spawn. Additionally, future studies could include receivers that are located in natal rivers to determine how often sea trout are returning to freshwater and how long they remain there, as well as trapping these returning fish to collect data on their salmon lice burdens to provide further evidence on the impacts of aquaculture on wild sea trout populations and their spatial use patterns.

The resulting information from this thesis has highlighted that Scottish sea trout populations have experienced a marked decline in recent decades and continue to be exposed to increasing threats that can limit their population recovery, particularly in the marine environment. As an apparent driving force behind the decline in sea trout populations, the

continued expansion of the Scottish aquaculture industry and the negative impacts associated with it, when coupled with rising climate change pressures, will increasingly impact already struggling wild sea trout population size and resilience. Therefore, it is important for the Scottish Government, the aquaculture industry and fisheries management organizations to develop improved monitoring and conservation measures that incorporate the driving forces identified here in order to successfully mitigate the loses in sea trout populations across Scotland.

Appendix 1: Supplementary Information for Chapter 2

(Drivers of population change in anadromous sea trout (*Salmo trutta*) in Scotland over the last 67 years)

The following supplementary information was compiled to report all significant results from each modelled Time Period. While the main purpose of this paper is to report on the main driving factors influencing sea trout populations across Scotland and thus we report on the general patterns from across the whole the SSSFT dataset, the modelling of individual Time Periods demonstrated that there were some significant relationships between sea trout abundance measures that only occurred in singular or intermittent periods. These relationships are not included in the main body of the paper for the sake of brevity, but could be considered important for more localised management organisations, hence the inclusion of these model outputs here as supplementary results.

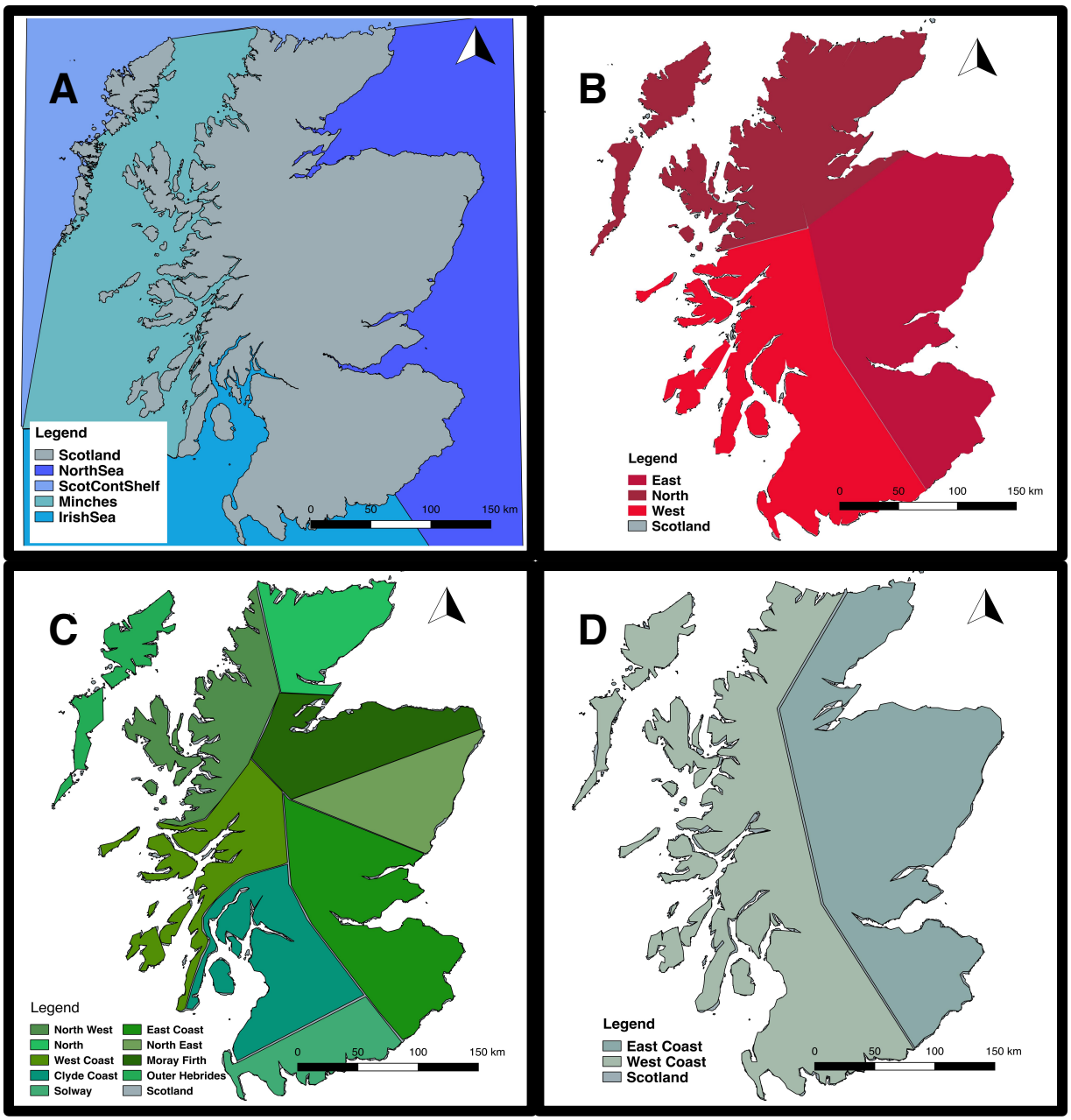


Figure A1.1A-D Map panel of specified geographic areas used in this study. A- sea temperature (°C) zones (N=5); B- rainfall (mm) and air temperature (°C) zones (N=3); C- Regions (N=9); D- Coastal divide (N=2).

Table A.1.1 – List of variables used in modelling in this study[µ]							
Genre	**Variable**	**Minimum Range**	**Maximum Range**	**Type/data per category**	**Reasoning**	**Source**	**Example(s)**
Measures of abundance	Sea trout catch	0.00	9391.00	Annual reported district sea trout abundance (67 years of data/district)		MSS[a]	
	Rate of change	-0.09	0.05	Change in district sea trout abundance over time; calculated for each district		Calculated by author	
	Proportional abundance	<0.001	9.00	Percentage of district annual sea trout abundance contributing to national annual total		Calculated by author	
	Population variance	27.62	1974.44	Standard deviation of District sea trout abundance; calculated for each district		Calculated by author	
Geographic	District	0.00	64.00	Geographic locations associated with a river or group of rivers designated by MSS	Changes in abundance between geographic location	MSS[a]	Youngson *et al*., 2002
	Region	0.00	9.00	Geographic locations associated containing multiple Districts designated by MSS		MSS[a]	Youngson *et al*., 2002
	Coast	0.00	2.00	Geographic locations separating Districts on the East and West coasts of Scotland assigned by author		Author	Jaffa 2018
River specific variables	Calcareous	0.00	61.82	% of calcareous geology within a catchment (1:250K scale)	River characteristics that have been shown to influence *S. trutta* populations	SEPA[Ω]	Solomon &Templeton, 1976
	River length	3.40	2859.37	the sum of all freshwater catchment river lengths in a District (km)		SEPA[Ω]	Bohlin *et al*., 2001; Armstrong *et al*., 2003

	Maximum altitude	265.00	1346.00	the highest point of altitude in a District		SEPA$^{\Omega}$	Bohlin *et al*., 2001
	Peat	0.00	85.97	% of peat geology within a District's catchment (1:625 scale)		SEPA$^{\Omega}$	Marttila *et al*., 2019
	Solid geology	7.02	87.69	% of solid geology at surface within a District's catchment, remaining % is drift geology		SEPA$^{\Omega}$	Armstrong *et al*., 2003
	Mean river gradient	1.97	37.92	mean slope of catchment in a District		SEPA$^{\Omega}$	Bohlin *et al*., 2001
	CSO/km	0.00	0.35	the number of combined sewer overflows (CSO) per km in District		SEPA$^{\Omega}$	Armstrong *et al*., 2003
	Flooding Likelihood (10 year)	0.53	8.18	the % of the District's catchment within a 1:10 year predictive flood area, derived from flood risk maps		SEPA$^{\Omega}$	Fausch 2007; May *et al*. 2017
	Percentage Lochs	0.00	4349.00	loch surface area as a percentage of the total District's catchment area	Important habitat for Scottish Sea trout	SEPA$^{\Omega}$, calculated by author	Campbell 1971
Climatic	Mean sea temperature	8.93	12.13	Annual mean sea temperature (°C); assigned by District location	Increasing temperatures can affect survival	Hughes *et al*., 2018	Honkanen *et al*., 2018
	I(Mean sea temperature^2)*	-	-	2nd order polynomial term of sea temperature (°C)	Negative effects from extreme temperatures	Author	Elliott & Elliott 2010
	Mean air temperature	5.88	9.05	Annual mean air temperature (°C); assigned by District location	Increasing temperatures can affect survival	Met Office $^{\lambda}$	Isaak *et al*., 2012

	I(Mean air temperature^2)*	-	-	2nd order polynomial term of air temperature (°C)	Negative effects from extreme temperatures	Author	Isaak *et al*., 2012
	Mean winter rain	36.53	242.02	Mean rain per month (mm) calculated from October Year X to March Year Y	Affecting flow/discharge and temperature	Met Office [λ]	Honkanen *et al*., 2018
	I(Mean winter rain^2)*	-	-	2nd order polynomial term of mean winter rain (mm)	Effects from extremes, floods or droughts	Author	Warren *et al*., 2015
	Winter rain variance	11.11	31.29	Standard deviation of mean winter rain (only used in rate of change models)	Erratic changes effect long term population trends	Author	
	Mean summer rain	36.11	157.96	Mean rain per month (mm) calculated from April Year Y to September Year Y	Affecting flow/discharge and temperature	Met Office [λ]	Honkanen *et al*., 2018
	I(Mean summer rain^2)*	-	-	2nd order polynomial term of mean summer rain (mm)	Effects from extremes, floods or droughts	Author	Warren *et al*., 2015
	Summer rain variance	12.12	17.12	Standard deviation of mean summer rain (only used in rate of change models)	Erratic changes effect long term population trends	Author	
	Winter NAO	-1.78	1.72	Mean NAO per month calculated from October Year X to March Year Y	Influence on major weather events	Climate Research Unit[Φ]	Honkanen *et al*., 2018
	I(Winter NAO^2)*	-	-	2nd order polynomial term of winter NAO	Effects from extreme weather	Author	Sarafanov 2009

	Summer NAO	-1.78	1.45	Mean NAO per month calculated from April Year Y to September Year Y	Influence on major weather events	Climate Research Unit$^{\Phi}$	Honkanen *et al*., 2018
	I(Summer NAO^2)*	-	-	2nd order polynomial term of summer NAO	Effects from extreme weather	Author	Sarafanov 2009

$^{\mu}$ including potential drivers of change in salmonid populations used as model explanatory variables, their definitions, justification for inclusion, and examples of their importance as well as the source of the data used. (* - the 2nd order polynomial term of a variable that was included in the modelling process; ^{a} - Marine Scotland Science, 2019; $^{\Omega}$ - Scottish Environment Protection Agency, 2019; $^{\lambda}$ - Met Office, 2019; $^{\Phi}$ - Climate Research Unit, 2019; ^{b} – Scottish Government, 2019.

Table A1.2 List of separate Time Periods analysed in this study.

Year	Name
1952-1966	Time period 1966
1966-1978	Time period 1978
1978-1987	Time period 1987
1987-1990	Time period 1990
1990-2000	Time period 2000
2000-2008	Time period 2008
2008-2014	Time period 2014
2014-2018	Time period 2018
1952-2018	Full time series

Table A1.3 The total sea trout catch, total proportionate abundance, and overall rate of change in sea trout catch for each Region (N=9) included in this study from all years combined (1952-2018). Statistically significant rates of change are can be seen in **bold**.

Region	Total sea trout catch	Proportionate abundance	Rate of change
Clyde Coast	303727	0.127	**-0.026**
East	194630	0.082	**0.016**
Moray Firth	467722	0.196	**-0.011**
North	118598	0.050	0.004
North East	427333	0.179	**-0.002**
North West	249678	0.105	**-0.023**
Outer Hebrides	208606	0.087	**-0.001**
Solway	338676	0.142	**-0.025**
West Coast	76123	0.032	**-0.017**

Table A1.4 The total sea trout catch, total proportionate abundance, and overall rate of change in sea trout catch for each District (N=64) included in this study (1952-2018). Statistically significant rates of change are can be seen in **bold**.

District	Total sea trout catch	Proportionate abundance	Rate of change
Annan	84296	0.035	**-0.016**
Arnisdale	3641	0.002	**0.014**
Awe	12449	0.005	**-0.058**
Ayr	16164	0.007	**-0.053**
Baa	13236	0.006	**-0.008**
Beauly	54606	0.023	**-0.029**
Broom	4604	0.002	**-0.031**
Brora	15950	0.007	0.006
Carradale	8654	0.004	**-0.062**
Carron	14659	0.006	0.001
Clyde	132624	0.056	**-0.013**
Conon	52698	0.022	**-0.031**
Cree	27503	0.012	**-0.015**
Creed	66936	0.028	-0.001
Dee	116198	0.049	0.004
Deveron	89453	0.038	**-0.016**
Don	24769	0.010	**0.027**
Doon	16941	0.007	**-0.058**
Echaig	31900	0.013	**-0.011**
Ewe	71096	0.030	**-0.029**
Findcastle	45129	0.019	-0.002
Findhorn	18031	0.008	0.004
Forth	33785	0.014	**0.027**
Fyne	20367	0.009	**-0.055**
Girvan	33830	0.014	**-0.056**
Grudie	15623	0.007	**-0.012**
Gruinard	11425	0.005	**-0.037**
Hope	54608	0.023	0.000
Howmore	28535	0.012	**0.012**
Inver	3219	0.001	**-0.022**
Irvine	10467	0.004	**0.024**
Kanaird	4280	0.002	**-0.025**
Kinloch	969	0.000	**0.044**
Kirkaig	8443	0.004	**0.027**
Kyle of Sutherland	27392	0.011	**0.013**
Laggan	11970	0.005	**0.009**
Laxford	32680	0.014	**-0.030**
Leven	4738	0.002	0.005
Little Loch Broom	2515	0.001	0.002
Loch Long	6430	0.003	**-0.019**
Loch Roag	68006	0.029	-0.004
Lochy	18076	0.008	**-0.014**
Luce	15028	0.006	**-0.024**
Moidart	7621	0.003	**-0.038**
Morar	11956	0.005	**-0.085**
Nairn	8925	0.004	0.003
Naver	4056	0.002	**0.048**
Nell	8339	0.003	**-0.039**
Ness	40367	0.017	**-0.052**
Nith	199965	0.084	**-0.030**
North Esk	31916	0.013	**0.021**
Ormsary	4209	0.002	**-0.016**
Pennygown	3106	0.001	**-0.033**

Table A1.4 (continued). The total sea trout catch, total proportionate abundance, and overall rate of change in sea trout catch for each District (N=64) included in this study (1952-2018). Statistically significant rates of change are can be seen in **bold**.

District	Total sea trout catch	Proportionate abundance	Rate of change
Ruel	7224	0.003	**-0.039**
Shiel	29533	0.012	**-0.029**
Sligachan	6888	0.003	**-0.010**
Snizort	30688	0.013	**-0.027**
South Esk	98972	0.041	**-0.006**
Spey	203642	0.085	**0.010**
Stinchar	25556	0.011	**-0.055**
Tay	93209	0.039	0.001
Tweed	67636	0.028	**0.034**
Urr	11884	0.005	**-0.039**
Ythan	155478	0.065	**-0.014**

A1.1 Time Period 1966 (1952-1966)

A.1.1.1 Sea trout catch

River length and Region

The significant interaction between river length and Region highlighted regional differences in sea trout catch in the Time Period 1966 indicating that for similar river lengths there were statistically different numbers of sea trout caught in different Regions. This difference in sea trout catch was greater for longer river lengths. Three Regions (Clyde Coast, Solway, and North West) had a significant positive relationship between sea trout catch and river length (each returning a $P < 0.001$), while four Regions (East ($P = 0.008$), North ($P < 0.001$), North East ($P < 0.001$) and West Coast ($P = 0.005$)) (Table A1.5), had a significant negative relationship between catch and river length. A District with a long river length in the North West Region reported a significantly higher sea trout catch compared to a District with a similar river length in the North East Region. As river length declined, the strength of the effect of the interaction decreased. All other Regions (Outer Hebrides and Moray Firth) did not show a significant relationship between sea trout catch and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00 (see Methods for description).

Calcareous geology

Across all Districts, the percentage of calcareous geology within a District's catchment area was typified by a significant negative relationship with sea trout catch in Time Period 1966 ($P < 0.001$) (Table A1.5), indicating that as the percentage of calcareous geology increased, sea trout catch declined. The percentage of calcareous geology within a District's catchment ranged from 0 to 61.82% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Peatland dominance

The percentage of peatland within a District's catchment area was typified by a border line positive relationship with sea trout catch in Time Period 1966 ($P = 0.054$) (Table A1.5), indicating that as peatland dominance in a District increased, sea trout catch also increased. Peatland dominance within a District's catchment ranged from 0 to 85.97% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

A.1.1.2 Proportional abundance

River length and Region

The significant interaction between river length and Region highlighted regional differences in proportional abundance in Time Period 1966 indicating that for similar river lengths, there was a statistically different proportional abundance of sea trout caught in different Regions. Three Regions (Clyde Coast, Solway, and North West) had a significant positive relationship between proportional abundance and river length (each $P < 0.001$), while four Regions (East ($P = 0.012$), North ($P = 0.010$), North East ($P < 0.001$) and West Coast ($P = 0.002$)) had a significant negative relationship between proportional abundance and river length. A District with a long river length in the Solway Region supplied a significantly higher proportional abundance of captured sea trout towards the national annual catch compared to a District with a similar river length in the North East Region. As river length declined, the strength of the effect of the interaction decreased. All other Regions (Outer Hebrides and Moray Firth) did not show a significant relationship between proportional abundance and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00.

Calcareous geology

The percentage of calcareous geology within a District's catchment area was typified by a significant negative relationship with proportional abundance of sea trout in Time Period 1966 ($P < 0.001$) (Table A1.5), indicating that as the percentage of calcareous geology increased, the proportional abundance of sea trout decreased. The percentage of calcareous geology within a District's catchment ranged from 0 to 61.82% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

A.1.1.3 Rate of change

No significant drivers of sea trout population rate of change were identified in Time Period 1966.

Table A1.5.1 - Time Period 1966 Variable Selection (1952-1966)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P-value	Importance	Est±SE	P-value	Importance	Est±SE	P-value	Importance
Geographic Intercept (Region)	6.697±0.257	<0.001	only 1 model	0.125±0.012	<0.001	1.000	0.211±0.154	0.178	--
Coast	0.011±0.241	0.963	only 1 model	-0.001±0.011	0.591	0.400	-0.125±0.182	0.497	0.480
River Specific Intercept	6.496±0.037	<0.001	--	0.105±0.002	<0.001	--	0.116±0.078	0.147	--
Calcareous	-0.149±0.039	<0.001	1.000	-0.012±0.002	<0.001	1.000	0.006±0.031	0.858	0.090
Main River Length	0.601±0.047	<0.001	1.000	0.025±0.003	<0.001	1.000	0.178±0.079	0.029	1.000
Maximum Altitude	-0.336±0.051	<0.001	1.000	-0.012±0.003	<0.001	1.000	-0.010±0.042	0.809	0.110
Peat	-0.144±0.039	<0.001	1.000	-0.005±0.002	0.012	1.000	0.029±0.062	0.645	0.290
Solid Geology	-0.097±0.039	0.014	1.000	-0.003±0.002	0.174	0.820		dropped	
Mean River Gradient	-0.015±0.036	0.684	0.260	-0.001±0.002	0.7756	0.210		dropped	
CSO/km	0.007±0.023	0.765	0.260	0.011±0.002	<0.001	1.000		dropped	
Flood10	-0.001±0.015	0.929	0.150	-0.000±0.001	0.889	0.170	-0.111±0.101	0.2804	0.710
Prop Lochs		dropped			dropped		-0.054±0.088	0.541	0.400
Climatic Intercept	6.409±0.065	<0.001	--	0.091±0.003	<0.001	--	0.052±0.136	0.707	--
Sea Temperature	-0.033±0.044	0.438	0.530	0.000±0.001	0.905	0.100	-0.007±0.035	0.838	0.130
I(Sea Temperature^2)	0.176±0.035	<0.001	1.000	0.011±0.002	<0.001	1.000	0.071±0.112	0.528	0.420
Air Temperature		co-correlated			co-correlated			co-correlated	
I(Air Temperature^2)		co-correlated			co-correlated			co-correlated	
Winter Rain	-0.141±0.044	0.001	1.000	-0.009±0.002	<0.001	1.000		co-correlated	
I(Winter Rain^2)	0.008±0.023	0.720	0.210	0.003±0.002	0.191	0.860		co-correlated	
Summer Rain	0.004±0.019	0.844	0.090	-0.001±0.001	0.946	0.090	-0.007±0.034	0.848	0.130
I(Summer Rain^2)	-0.001±0.006	0.926	0.030	0.000±0.001	0.907	0.100	-0.004±0.023	0.825	0.120
Winter NAO	0.024±0.039	0.534	0.420	0.000±0.001	0.848	0.110		co-correlated	
I(Winter NAO^2)	-0.015±0.027	0.581	0.390		dropped			co-correlated	
Summer NAO	-0.000±0.007	0.947	0.030	0.000±0.001	0.856	0.110		co-correlated	
I(Summer NAO^2)	-0.009±0.018	0.608	0.340	0.000±0.000	0.869	0.110		co-correlated	

Table A1.5.2 - Time Period 1966 Averaged Model (1952 -1966)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Intercept (Clyde Coast)	6.847±0.121	<0.001	1.000	0.138±0.009	<0.001	1.000	--	--	--
Region East	-1.478±0.324	<0.001	1.000	-0.063±0.016	<0.001	1.000	--	--	--
Region Moray Firth	-0.437±0.249	0.079	1.000	-0.032±0.001	0.004	1.000	--	--	--
Region North	-1.689±0.290	<0.001	1.000	-0.083±0.014	<0.001	1.000	--	--	--
Region North East	0.504±0.243	0.039	1.000	0.035±0.012	0.004	1.000	--	--	--
Region North West	1.081±0.297	<0.001	1.000	0.033±0.018	0.062	1.000	--	--	--
Region Outer Hebrides	0.510±0.345	0.140	1.000	0.051±0.019	0.007	1.000	--	--	--
Region Solway	0.386±0.147	0.009	1.000	0.037±0.011	0.001	1.000	--	--	--
Region West Coast	-1.235±0.144	>0.001	1.000	-0.074±0.012	<0.001	1.000	--	--	--
Coast	--	--	--	--	--	--	--	--	--
Calcareous	-0.169±0.044	<0.001	1.000	-0.013±0.002	<0.001	1.000	--	--	--
River Length	0.704±0.119	<0.001	1.000	0.071±0.022	0.001	1.000	0.112±0.102	0.278	0.700
Altitude	-0.003±0.020	0.868	0.100	-0.001±0.001	0.720	0.200	--	--	--
Peat	0.081±0.042	0.054	1.000	-0.001±0.001	0.724	0.220	--	--	--
Solid Geology	-0.026±0.037	0.477	0.460	-0.001±0.001	0.665	0.260	--	--	--
CSO/km	--	--	--	-0.004±0.007	0.556	0.410	--	--	--
Mean River Gradient	--	--	--	--	--	--	--	--	--
Flood10	--	--	--	--	--	--	--	--	--
Proportion Lochs	--	--	--	--	--	--	--	--	--
Sea Temperature	-0.104±0.080	0.196	0.790		dropped		--	--	--
I(Sea Temperature^2)	0.005±0.018	0.796	0.210	0.000±0.001	0.796	0.140	--	--	--
Air Temperature	--	--	--	--	--	--	--	--	--
I(Air Temperature^2)	--	--	--	--	--	--	--	--	--
Winter Rain		dropped		-0.001±0.001	0.818	0.130	--	--	--
I(Winter Rain^2)	--	--	--	0.000±0.001	0.862	0.080	--	--	--

Table A1.5.2 (continued) - Time Period 1966 Averaged Model (1952 -1966)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Summer Rain	--	--	--	--	--	--	--	--	--
I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Winter NAO	--	--	--	--	--	--	--	--	--
I(Winter NAO^2)	--	--	--	--	--	--	--	--	--
Summer NAO	--	--	--	--	--	--	--	--	--
I(Summer NAO^2)	--	--	--	--	--	--	--	--	--
Population Variance	--	--	--	--	--	--	0.107±0.102	0.300	0.680
Region East: Main River	-0.388±0.145	0.008	1.000	-0.057±0.022	0.012	1.000	--	--	--
Region Moray Firth: River Length	-0.243±0.158	0.125	1.000	-0.037±0.023	0.122	1.000	--	--	--
Region North: River Length	-1.743±0.458	<0.001	1.000	-0.075±0.029	0.010	1.000	--	--	--
Region North East: River Length	-1.309±0.219	<0.001	1.000	-0.120±0.019	<0.001	1.000	--	--	--
Region North West: River Length	3.296±0.532	<0.001	1.000	0.117±0.034	0.001	1.000	--	--	--
Region Outer Hebrides: River Length	0.648±0.545	0.235	1.000	0.034±0.034	0.331	1.000	--	--	--
Region Solway: Main River	2.365±0.364	<0.001	1.000	0.165±0.028	<0.001	1.000	--	--	--
Region West Coast: River Length	-0.613±0.219	0.005	1.000	-0.073±0.023	0.002	1.000	--	--	--
River Length: Winter Rain		dropped			dropped		--	--	--
River Length: I(Winter Rain^2)	--	--	--	--	--	--	--	--	--
River Length: Summer Rain	--	--	--	--	--	--	--	--	--
River Length: I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Mean Gradient:Winter Rain	--	--	--	--	--	--	--	--	--
Mean Gradient: I(Winter Rain^2)	--	--	--	--	--	--	--	--	--
Mean Gradient:Summer Rain	--	--	--	--	--	--	--	--	--
Mean Gradient: I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Prop Lochs:Winter Rain	--	--	--	--	--	--	--	--	--

Table A1.5.2 (continued) - Time Period 1966 Averaged Model (1952 -1966)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
PropLochs: I(WinterRain^2)	--	--	--	--	--	--	--	--	--
Prop Lochs:Summer Rain	--	--	--	--	--	--	--	--	--
Prop Lochs: I(Summer Rain^2)	--	--	--	--	--	--	--	--	--

A1.2 Time Period 1978 (1966-1978)

A1.2.1 Sea trout catch

River length and Region

A significant interaction between river length and Region highlighted regional differences in sea trout catch Time Period 1978, indicating that for similar river lengths, there were statistically different numbers of sea trout caught in different Regions. This differences in sea trout catch was greater for longer river lengths. Three Regions (Clyde Coast, Solway, and North West) had significant positive relationships between sea trout catch and river length ($P < 0.001$), while two Regions (North ($P = 0.019$) and North East ($P = 0.001$)) had significant negative relationships between sea trout catch and river length (Table A1.6). The East Region reported a borderline significant negative relationship between catch and river length ($P = 0.052$). A District with a long river length in the North West Region reported a significantly higher sea trout catch compared to a District with a similar river length in the North East Region. As river length declined, the strength of the effect of the interaction decreased. All other Regions (West Coast, Outer Hebrides and Moray Firth) showed no significant relationship between sea trout catch and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00 (see Methods for description).

Polynomial of summer NAO

The relationship between the polynomial of mean summer NAO values (North Atlantic Oscillation Index) (Table A1.1) and sea trout catch across all Districts was typified by a significant positive relationship ($P = 0.013$) (Table A1.6). For example, predicted sea trout catch increased as summer NAO values increased, but there was a small decline in catch as NAO values reached 1.00. Summer NAO values ranged from -1.1 to 0.80 in Time Period 1978 (Table A1.7). The Importance Value assigned to this model term by the model dredging process was 1.00.

Winter NAO

The relationship between mean winter NAO values and sea trout catch across all Districts was typified by a significant positive relationship ($P = 0.009$) (Table A1.6). The data suggest that as winter NAO increased, sea trout catch also increased. Winter NAO values ranged from -1.72 to 0.77 in Time Period 1978 (Table A1.7). This Time Period reported

the lowest mean winter NAO values of the time series, indicating that climatic events were colder and calmer relative to other Time Periods. The Importance Value assigned to this model term by the model dredging process was 1.00.

Air temperature

The relationship between annual mean air temperature (C°) and sea trout catch across all Districts was typified by a significant negative relationship across all Districts (P = 0.001) (Table A1.6), indicating that as air temperature increased, sea trout catch declined. Mean air temperatures ranged from 6.35°C to 8.26°C in Time Period 1978 (Table A1.7). The Importance Value assigned to this model term by the model dredging process was 1.00.

Sea temperature

The relationship between annual mean sea temperature (C°) and sea trout catch across all Districts was typified by a significant positive relationship (P = 0.019) (Table A1.6), indicating that as sea temperature increased, sea trout catch also increased. Mean sea temperatures ranged from 9.43°C to 11.52°C in Time Period 1978 (Table A1.7). The Importance Value assigned to this model term by the model dredging process was 1.00.

Winter rainfall

The relationship between mean winter rainfall and sea trout catch was typified by a significant negative relationship (P = 0.032) (Table A1.6), indicating that as winter rainfall increased, sea trout catch declined. Mean winter rainfall values ranged from 36.53mm to 183.10mm (Table A1.7) The Importance Value assigned to this model term by the model dredging process was 1.00.

Percent of solid geology

The percentage of solid geology within a District's catchment area was typified by a significant negative relationship with sea trout catch across all Districts in Time Period 1978 (P =0.002) (Table A1.6). The data indicated that as the percentage of solid geology in a catchment increased, sea trout catch declined. The percentage of solid geology within a District's catchment ranged from 7.02 to 87.69% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

A1.2.2 Proportional abundance

River length and Region

A significant interaction between river length and Region highlighted regional differences in proportional abundance of sea trout Time Period 1978, indicating that for similar river lengths there was a statistically different proportional abundance of sea trout caught in different Regions. This difference in proportional abundance was greater for longer river lengths. Three Regions (Clyde Coast, Solway, and North West) had a significant positive relationship between proportional abundance and river length ($P < 0.001$), while five Regions (East, Moray Firth, North, North East and West Coast ($P < 0.001$) (Table A1.6)) had a significant negative relationship between proportional abundance and river length. A District with a long river length in the Solway Region accounted for a significantly larger proportion of captured sea trout compared to a District with a similar river length in the North East Region. As river length declined, the strength of the effect of the interaction decreased. The Outer Hebrides Region did not show a significant relationship between proportional abundance and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00.

Calcareous geology

Across all Districts, the percentage of calcareous geology within a District's catchment area was typified by a significantly negative relationship with proportional abundance during Time Period 1978 ($P = 0.013$) (Table A1.6), indicating that as the percentage of calcareous geology in a District increased, the proportion of sea trout decreased. The percentage of calcareous geology within a District's catchment ranged from 0 to 61.82% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Percent of solid geology

The percentage of solid geology within a District's catchment area was typified by a significant negative relationship with proportional abundance of sea trout in Time Period 1978 ($P = 0.024$) (Table A1.6), indicating that as the percentage of solid geology in a District increased, the proportion of sea trout decreased. The percentage of solid geology within a District's catchment ranged from 7.02 to 87.69% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Polynomial of winter rainfall

In Time Period 1978, the relationship between proportional abundance and the second order polynomial term of mean winter rainfall was typified by a significant relationship across all Districts ($P = 0.013$) (Table A1.6). Although predicted proportional abundance

initially declines as mean monthly winter rainfall increases, there is a slight increase in proportional abundance after mean rainfall exceeds 150 mm per month. Mean winter rainfall values range from 36.53mm to 183.10mm in Time Period 1978 (Table A1.7). The Importance Value assigned to this model term by the model dredging process was 1.00.

A1.2.3 Rate of change

No significant drivers of sea trout population rate of change were identified in Time Period 1978.

Table A1.6.1 - Time Period 1978 Variable Selection (1966-1978)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P-value	Importance	Est±SE	P-value	Importance	Est±SE	P-value	Importance
Geographic Intercept (Region)	6.293±0.196	<0.001	1.000	0.109±0.013	<0.001	1.000	0.564±0.903	0.535	only 1 model
Coast	0.042±0.169	0.804	0.290	-0.005±0.012	0.650	0.360	-0.473±0.854	0.582	only 1 model
River Specific Intercept	6.131±0.042	<0.001	--	0.101±0.002	<0.001	--	0.071±0.113	0.537	--
Calcareous		dropped		-0.006±0.002	0.026	1.000	0.077±0.115	0.506	0.470
Main River Length	0.730±0.049	<0.001	1.000	0.034±0.003	<0.001	1.000		dropped	
Maximum Altitude	-0.273±0.053	<0.001	1.000	-0.005±0.003	0.141	0.870		dropped	
Peat	-0.134±0.044	0.002	1.000	-0.004±0.003	0.157	0.860	-0.005±0.034	0.896	0.070
Solid Geology	-0.192±0.044	<0.001	1.000	-0.007±0.002	0.003	1.000	0.019±0.063	0.763	0.170
Mean River Gradient	-0.003±0.023	0.910	0.140		dropped		0.005±0.035	0.891	0.070
CSO/km	0.002±0.017	0.905	0.140	0.012±0.002	<0.001	1.000	-0.010±0.048	0.838	0.080
Flood10	-0.005±0.021	0.814	0.160	-0.001±0.002	0.559	0.410	-0.047±0.108	0.664	0.280
Prop Lochs	-0.009±0.027	0.742	0.210	-0.004±0.003	0.249	0.750	0.020±0.079	0.799	0.090
Climatic Intercept	5.678±0.096	<0.001	--	0.080±0.005	<0.001	--	0.096±0.143	0.509	--
Sea Temperature	0.327±0.068	<0.001	1.000	-0.002±0.003	0.581	0.390		dropped	
I(Sea Temperature^2)	0.390±0.055	<0.001	1.000	0.016±0.003	<0.001	1.000	-0.024±0.086	0.788	0.281
Air Temperature	-0.221±0.071	0.002	1.000	-0.001±0.002	0.782	0.150		co-correlated	
I(Air Temperature^2)	-0.056±0.052	0.285	0.710	-0.001±0.002	0.591	0.350		co-correlated	
Mean Winter Rain	-0.254±0.066	<0.001	1.000	-0.016±0.003	<0.001	1.000		dropped	
I(Mean Winter Rain^2)	0.147±0.046	0.001	1.000	0.007±0.002	0.002	1.000		dropped	
Mean Summer Rain		co-correlated			co-correlated			co-correlated	
I(Mean Summer Rain^2)		co-correlated			co-correlated			co-correlated	

Table A1.6.1 (continued) - Time Period 1978 Variable Selection (1966-1978)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P-value	Importance	Est±SE	P-value	Importance	Est±SE	P-value	Importance
Winter NAO	0.182±0.059	0.002	1.000	0.001±0.003	0.580	0.360		co-correlated	
I(Winter NAO^2)	-0.002±0.013	0.882	0.120	-0.001±0.002	0.488	0.460		co-correlated	
Summer NAO	0.017±0.036	0.641	0.310	-0.000±0.001	0.799	0.130		co-correlated	
I(Summer NAO^2)	0.052±0.036	0.149	0.880	-0.000±0.001	0.922	0.030		co-correlated	

Table A1.6.2 - Time Period 1978 Averaged Model (1966-1978)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Intercept (Clyde Coast)	5.803±0.193	<0.001	1.000	0.115±0.006	<0.001	1.000	--	--	--
Region East	-0.970±0.511	0.058	1.000	-0.103±0.019	<0.001	1.000	--	--	--
Region Moray Firth	0.460±0.392	0.242	1.000	-0.014±0.019	0.198	1.000	--	--	--
Region North	-0.371±0.393	0.347	1.000	-0.053±0.012	<0.001	1.000	--	--	--
Region North East	0.954±0.448	0.034	1.000	0.004±0.015	0.811	1.000	--	--	--
Region North West	1.935±0.359	<0.001	1.000	0.069±0.015	<0.001	1.000	--	--	--
Region Outer Hebrides	1.071±0.447	0.017	1.000	0.041±0.017	0.018	1.000	--	--	--
Region Solway	0.711±0.162	<0.001	1.000	0.067±0.008	<0.001	1.000	--	--	--
Region West Coast	-0.561±0.210	0.008	1.000	-0.048±0.007	<0.001	1.000	--	--	--
Coast	--	--	--	--	--	--	--	--	--
Calcareous	--	--	--	-0.006±0.002	0.013	1.000	--	--	--
River Length	0.825±0.123	<0.001	1.000	0.075±0.006	<0.001	1.000	--	--	--
Altitude	-0.075±0.067	0.270	0.750	-0.001±0.001	0.794	0.210	--	--	--
Peat		dropped			dropped		--	--	--

Table A1.6.2 (continued) - Time Period 1978 Averaged Model (1966-1978)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Solid Geology	-0.125±0.041	0.002	1.000	-0.004±0.002	0.024	1.000	--	--	--
CSO/km	--	--	--	dropped	--	--	--		
Mean River Gradient	--	--	--	--	--	--	--	--	--
Flood10	--	--	--	--	--	--	--	--	--
Proportion Lochs	--	--	--	--	--	--	--	--	--
Sea Temperature	0.333±0.142	0.019	1.000	-0.001±0.002	0.834	0.190	--	--	--
I(Sea Temperature^2)	-0.006±0.027	0.829	0.110		dropped		--	--	--
Air Temperature	-0.230±0.072	0.002	1.000	--	--	--	--	--	--
I(Air Temperature^2)				--	--	--	--	--	--
Winter Rain	-0.155±0.072	0.032	1.000	-0.014±0.003	<0.001	1.000	--	--	--
I(Winter Rain^2)	0.057±0.052	0.271	0.730	0.005±0.002	0.013	1.000	--	--	--
Summer Rain	--	--	--	--	--	--	--	--	--
I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Winter NAO	0.139±0.053	0.009	1.000	--	--	--	--	--	--
I(Winter NAO^2)	--	--	--	--	--	--	--	--	--
Summer NAO	0/029±0.041	0.476	0.500	--	--	--	--	--	--
I(Summer NAO^2)	0.066±0.027	0.013	1.000	--	--	--	--	--	--
Population Variance	--	--	--	--	--	--	--	--	--
Region East: Main River	-0.318±0.164	0.053	1.000	-0.049±0.009	<0.001	1.000	--	--	--
Region Moray Firth: River Length	-0.267±0.175	0.127	1.000	-0.043±0.009	<0.001	1.000	--	--	--
Region North: River Length	-1.105±0.471	0.019	1.000	-0.075±0.021	<0.001	1.000	--	--	--
Region North East: River Length	-0.823±0.260	0.002	1.000	-0.102±0.013	<0.001	1.000	--	--	--
Region North West: River Length	3.940±0.593	<0.001	1.000	0.133±0.027	<0.001	1.000	--	--	--

Table A1.6.2 (continued) - Time Period 1978 Averaged Model (1966-1978)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Region Outer Hebrides:River Length	0.462±0.616	0.454	1.000	-0.009±0.028	0.747	1.000	--	--	--
Region Solway: Main River	2.700±0.402	<0.001	1.000	0.229±0.018	<0.001	1.000	--	--	--
Region West Coast: River Length	0.088±0.255	0.730	1.000	-0.049±0.011	<0.001	1.000	--	--	--
River Length: Winter Rain	0.005±0.025	0.845	0.110	-0.002±0.003	0.437	0.560	-0.005±0.010	0.622	only 1 model
River Length: I(Winter Rain^2)	-0.003±0.014	0.827	0.110	-0.001±0.001	0.796	0.130	--	--	--
River Length:Summer Rain	--	--	--	--	--	--	--	--	--
River Length: I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Mean Gradient:Winter Rain	--	--	--	--	--	--	--	--	--
Mean Gradient:I(Winter Rain^2)	--	--	--	--	--	--	--	--	--
Mean Gradient:Summer Rain	--	--	--	--	--	--	--	--	--
Mean Gradient:I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Prop Lochs:Winter Rain	--	--	--	--	--	--	--	--	--
PropLochs:I(WinterRain^2)	--	--	--	--	--	--	--	--	--
Prop Lochs:Summer Rain	--	--	--	--	--	--	--	--	--
Prop Lochs:I(Summer Rain^2)	--	--	--	--	--	--	--	--	--

Table A1.7 - Maximum and minimum ranges for climatic variables for each Time Period.												
Variable	1966 Time Period			1978 Time Period			1987 Time Period			2000 Time Period		
	Min Range	Max Range	Mean ± SE	Min Range	Max Range	Mean ± SE	Min Range	Max Range	Mean ± SE	Min Range	Max Range	Mean ± SE
Air temperature (°C)	6.13	8.52	7.11±0.02	6.35	8.26	7.16±0.02	5.88	8.14	6.97±0.02	6.56	8.61	7.52±0.02
Sea temperature (°C)	9.25	12.02	10.52±0.02	9.43	11.52	10.52±0.02	8.93	11.23	10.29±0.02	9.49	11.76	10.63±0.02
Summer rain (mm)	36.12	137.38	99.75±0.68	41.53	121.35	86.05±0.61	44.03	157.97	96.27±1.05	42.77	139.15	94.78±0.82
Winter rain (mm)	45.42	186.43	122.77±1.17	36.53	183.1	127.04±1.17	59.03	213.87	147.97±1.59	57.48	214.27	155.20±1.67
Summer NAO	-0.6	1.32	0.11±0.01	-1.1	0.8	-0.14±0.02	-0.46	0.58	-0.12±0.01	-1.56	1.06	-0.29±0.03
Winter NAO	-1.28	1.53	0.04±0.02	-1.72	0.77	0.00+0.02	-0.47	1.67	0.27±0.03	-1.8	1.59	0.42±0.03
Variable	2008 Time Period			2014 Time Period			2018 Time Period					
	Min Range	Max Range	Mean ± SE	Min Range	Max Range	Mean ± SE	Min Range	Max Range	Mean ± SE			
Air temperature (°C)	7.01	8.84	8.01±0.02	6.2	9.05	7.7±0.03	7.26	9.05	8.01±0.05			
Sea temperature (°C)	10.1	12.13	11.03±0.02	10.07	12.03	10.94±0.02	10.27	12.03	10.98±0.03			
Summer rain (mm)	39.17	124.78	94.22±0.79	49.07	137.87	104.62±1.01	43.4	122.58	99.82±1.12			
Winter rain (mm)	61.42	221.22	142.58±1.58	50.63	211.57	146.98±1.98	55.25	211.57	150.18±2.62			
Summer NAO	-1.72	0.25	-0.61±0.03	-1.78	1.13	-0.66±0.05	-0.59	1.45	0.39±0.04			
Winter NAO	-0.79	1.21	-0.01±0.03	-1.78	1.73	-0.11±0.06	-1.23	1.62	0.41±0.05			

A1.3 Time Period 1987 (1978-1987)

A1.3.1 Sea trout catch

River length and Region

A significant interaction between river length (km) and Region highlighted regional differences in sea trout catch in Time Period 1987, indicating that for similar river lengths, there were statistically different numbers of sea trout caught in different Regions. This difference in sea trout catch was greater for longer river lengths. Three Regions (Clyde Coast, Solway, and North West) had a significant positive relationship between sea trout catch and river length (each reporting a $P < 0.001$), while five Regions (East ($P < 0.001$), Moray Firth ($P = 0.021$), North ($P < 0.001$), North East ($P < 0.001$) and West Coast ($P < 0.001$)) (Table A1.8) had a significant negative relationship between catch and river length. A District with a long river length in the North West Region reported a significantly higher sea trout catch compared to a District with a similar river length in the North East Region. As river length declined, the strength of the effect of this interaction declined. Only the Outer Hebrides Region showed no significant relationship between sea trout catch and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00 (see Methods for description).

Polynomial of winter rainfall

The relationship between sea trout catch and the polynomial of mean winter (mm) was typified by a significant relationship in Time Period 1987 ($P = 0.009$) (Table A1.8). Sea trout catches declined as winter rainfall increased to a monthly mean of 150mm, but showed a slight increase again when rainfall reached a monthly mean of over 200mm. Mean winter rainfall values ranged from 59.03mm to 213.87mm during Time Period 1987 (Table A1.7). The Importance Value assigned to this model term by the model dredging process was 1.00.

Mean river gradient

The relationship between the mean gradient of a District with sea trout catch was typified by a significant positive relationship in Time Period 1978 ($P = 0.005$) (Table A1.8), indicating that as the mean gradient of a river increases, so did sea trout catch. Mean river gradient values ranged from 1.97 to 37.92 (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Peatland dominance

The percentage of peatland within a District's catchment area had a significant positive relationship with sea trout catch in Time Period 1987 (P= 0.004) (Table A1.8), indicating that as peatland dominance increased, so did sea trout catch. Peatland dominance within a District's catchment ranged from 0 to 85.97% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Solid geology

The percentage of solid geology within a District's catchment area had a significantly negative relationship with sea trout catch in Time Period 1987 (P = 0.009) (Table A1.8), indicating that as the percent of solid geology increased, sea trout catch declined. The percentage of solid geology within a District's catchment ranged from 7.02 to 87.69% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

A1.3.2 Proportional abundance

River length and Region

A significant interaction between river length and Region highlighted regional differences in the proportional abundance of sea trout in Time Period 1987, indicating that for similar river lengths, there was a statistically different proportional abundance of sea trout caught in different Regions. This difference in proportional abundance was greater for longer river lengths. Three Regions (Clyde Coast, Solway, and North West) had a significant positive relationship between proportional abundance and river length (each P <0.001), while four Regions (East (P < 0.001), North (P = 0.021), North East (P <0.001) and West Coast (P <0.001) (Table A1.8)) had a significant negative relationship between proportional abundance and river length. A District with a long river length in the Solway Region reported a significantly higher proportional abundance compared to a District with a similarly sized river in the North East Region. As river length declined, the strength of the effect of the interaction decreased. All other Regions (Outer Hebrides and Moray Firth) did not show a significant relationship between proportional abundance and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00.

River length and winter rainfall

An interaction between District river length and mean winter rainfall was typified by a significant relationship between proportional abundance and mean winter rainfall in Time

Period 1987 (P <0.001) (Table A1.8). For example, a higher proportional abundance was caught in longer rivers when winter rainfall levels were high than when rainfall levels were low. However, significantly lower proportions of sea trout were reported in smaller rivers when rainfall was high. In these same smaller rivers, higher proportional abundance was reported as winter rainfall levels declined. Mean winter rainfall values ranged from 59.03mm to 213.87mm in Time Period 1987 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Mean river gradient and winter rainfall

An interaction between a District's mean river gradient and the polynomial of mean winter rainfall was typified by a significantly negative relationship between winter rainfall and proportional abundance in Time Period 1987 (P = 0.037) (Table A1.8). For example, a significantly higher proportional abundance was returned in rivers with a lower mean gradient when winter rainfall was high than when rainfall was low. As mean gradient increased, the proportional abundance of sea trout declined regardless of winter rainfall. Mean winter rainfall values ranged from 59.03mm to 213.87mm in Time Period 1987 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Peatland dominance

In Time Period 1987, the percentage of peatland within a District's catchment area had a significantly positive relationship with proportional abundance (P= 0.016) (Table A1.8), indicating that as peatland dominance in a District increased, so did the predicted proportional abundance of sea trout. Peatland dominance within a District's catchment ranged from 0 to 85.97% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Percentage of lochs

In Time Period 1987, the percentage of lochs within a District's catchment area had a significantly negative relationship with proportional abundance (P =0.002) (Table A1.8), indicating that as the percentage of lochs within a Districted increased, the predicted proportional abundance of sea trout decreased. The percentage of a District comprised of lochs ranged from 0.00 to 43.49% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

A1.3.3 Rate of change

Mean river gradient

A significant negative relationship was found between the mean gradient of Districts and rate of change in sea trout populations in Time Period 1987 ($P < 0.001$) (Table A1.8), indicating that as the mean gradient of a District increased, the predicted rate of change in sea trout populations within that same district decreased. Mean river gradient values ranged from 1.97 to 37.92 (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Table A1.8.1 - Time Period 1987 Variable Selection (1978-1987)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P-value	Importance	Est±SE	P-value	Importance	Est±SE	P-value	Importance
Geographic Intercept (Region)	5.971±0.244	<0.001	--	0.094±0.015	<0.001	--	-0.094±0.151	0.539	--
Coast	0.076±0.214	0.721	0.320	-0.007±0.014	0.624	0.380	-0.044±0.147	0.539	0.289
Region	5.971±0.244	<0.001	1.000	0.094±0.015	<0.001	1.000		dropped	
River Specific Intercept	6.130±0.047	<0.001	--	0.099±0.003	<0.001	--	-0.121±0.093	0.200	--
Calcareous	0.001±0.013	0.935	0.060	-0.000±0.001	0.869	0.120	-0.006±0.035	0.865	0.090
Main River Length	0.618±0.067	<0.001	1.000	0.035±0.003	<0.001	1.000		dropped	
Maximum Altitude	-0.044±0.069	0.530	0.410	0.000±0.001	0.928	0.110		dropped	
Peat	-0.195±0.054	<0.001	1.000	-0.007±0.003	0.023	1.000	-0.025±0.068	0.720	0.260
Solid Geology	-0.288±0.051	<0.001	1.000	-0.010±0.003	<0.001	1.000		dropped	
Mean River Gradient	-0.222±0.068	0.001	1.000	-0.006±0.004	0.131	0.870	-0.376±0.113	0.001	1.000
CSO/km	-0.011±0.033	0.727	0.280		Dropped			dropped	
Flood10	-0.035±0.052	0.508	0.410	-0.002±0.003	0.571	0.360	-0.044±0.088	0.621	0.340
Prop Lochs	-0.002±0.017	0.886	0.070	-0.006±0.004	0.149	0.820	-0.085±0.120	0.481	0.490
Climatic Intercept	5.778±0.139	<0.001	--	0.081±0.005	<0.001	--	-0.169±0.139	0.235	--
Sea Temperature	0.172±0.072	0.017	1.000	0.000±0.001	0.934	0.080	-0.011±0.048	0.829	0.140
I(Sea Temperature^2)	0.255±0.062	<0.001	1.000	-0.012±0.003	<0.001	1.000	0.028±0.084	0.744	0.189
Air Temperature		dropped		-0.001±0.002	0.792	0.170		co-correlated	
I(Air Temperature^2)	-0.119±0.051	0.019	1.000	-0.004±0.003	0.129	0.900		co-correlated	
Mean Winter Rain	-0.350±0.074	<0.001	1.000	-0.024±0.004	<0.001	1.000	-0.012±0.050	0.817	0.146
I(Mean Winter Rain^2)	0.160±0.057	0.005	1.000	0.010±0.003	<0.001	1.000	0.014±0.042	0.738	0.194
Mean Summer Rain	0.015±0.047	0.752	0.220	-0.001±0.001	0.875	0.090		co-correlated	
I(Mean Summer Rain^2)	0.039±0.047	0.401	0.580	0.000±0.001	0.921	0.080		co-correlated	
Winter NAO	0.004±0.022	0.862	0.100	-0.005±0.004	0.216	0.820		co-correlated	

Table A1.8.1 (continued) - Time Period 1987 Variable Selection (1978-1987)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P-value	Importance	Est±SE	P-value	Importance	Est±SE	P-value	Importance
I(Winter NAO^2)	0.006±0.022	0.781	0.140	-0.001±0.001	0.931	0.080		co-correlated	
Summer NAO	-0.178±0.114	0.119	0.860	-0.001±0.001	0.894	0.090		co-correlated	
I(Summer NAO^2)	0.093±0.062	0.132	0.860		dropped			co-correlated	

Table A1.8.2 - Time Period 1987 Averaged Model (1978-1987)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Intercept (Clyde Coast)	5.841±0.112	<0.001	1.000	0.093±0.005	<0.001	1.000	--	--	--
Region East	-0.729±0.419	0.082	1.000	-0.054±0.019	0.005	1.000	--	--	--
Region Moray Firth	-0.083±0.225	0.713	1.000	0.001±0.010	0.908	1.000	--	--	--
Region North	-0.711±0.262	0.007	1.000	-0.016±0.012	0.183	1.000	--	--	--
Region North East	0.507±0.333	0.128	1.000	0.039±0.015	0.013	1.000	--	--	--
Region North West	2.432±0.350	<0.001	1.000	0.016±0.002	<0.001	1.000	--	--	--
Region Outer Hebrides	0.377±0.382	0.326	1.000	0.063±0.020	0.002	1.000	--	--	--
Region Solway	1.159±0.173	<0.001	1.000	0.098±0.008	<0.001	1.000	--	--	--
Region West Coast	-0.807±0.169	<0.001	1.000	-0.032±0.008	<0.001	1.000	--	--	--
Coast	--	--	--	--	--	--			
Calcareous	--	--	--	--	--	--	--	--	--
River Length	1.037±0.136	<0.001	1.000	0.055±0.006	<0.001	1.000	--	--	--
Altitude	--	--	--	--	--	--	--	--	--
Peat	0.172±0.059	0.004	1.000	0.006±0.003	0.016	1.000	--	--	--
Solid Geology	-0.101±0.044	0.020	1.000	-0.001±0.002	0.627	0.320	--	--	--
CSO/km	--	--	--	--	--	--	--	--	--

Table A1.8.2 (continued) - Time Period 1987 Averaged Model (1978-1987)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Mean River Gradient	0.205±0.072	0.005	1.000	0.016±0.004	<0.001	1.000	-0.425±0.095	<0.001	only 1 model
Flood10	--	--	--	--	--	--			
Proportion Lochs	--	--	--	-0.010±0.003	0.002	1.000	--	--	--
Sea Temperature	-0.001±0.019	0.942	0.030		dropped		--	--	--
I(Sea Temperature^2)	-0.002±0.015	0.900	0.060	-0.001±0.001	0.937	0.040	--	--	--
Air Temperature	-0.006±0.023	0.808	0.110		dropped		--	--	--
I(Air Temperature^2)	-0.009±0.023	0.706	0.210	-0.001±0.001	0.874	0.080	--	--	--
Winter Rain	-0.205±0.077	0.008	1.000	-0.018±0.004	<0.001	1.000	--	--	--
I(Winter Rain^2)	0.140±0.068	0.039	1.000	0.005±0.003	0.090	1.000	--	--	--
Summer Rain	--	--	--	--	--	--	--	--	--
I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Winter NAO	--	--	--	0.002±0.002	0.336	0.650	--	--	--
I(Winter NAO^2)	--	--	--	--	--	--	--	--	--
Summer NAO	-0.001±0.008	0.939	0.030	--	--	--	--	--	--
I(Summer NAO^2)	dropped	--	--	--	--	--	--		
Population Variance	--	--	--	--	--	--	-0.040±0.118	0.733	only 1 model
Region East: Main River	-0.812±0.219	<0.001	1.000	-0.051±0.011	<0.001	1.000	--	--	--
Region Moray Firth: River Length	-0.474±0.205	0.021	1.000	-0.007±0.001	0.449	1.000	--	--	--
Region North: River Length	-2.273±0.556	<0.001	1.000	-0.058±0.025	0.021	1.000	--	--	--
Region North East: River Length	-1.481±0.296	<0.001	1.000	-0.124±0.014	<0.001	1.000	--	--	--
Region North West: River Length	5.239±0.624	<0.001	1.000	0.322±0.036	<0.001	1.000	--	--	--
Region Outer Hebrides:River Length	-0.892±0.655	0.174	1.000	0.026±0.034	0.442	1.000	--	--	--

Table A1.8.2 (continued) - Time Period 1987 Averaged Model (1978-1987)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Region Solway: Main River	2.914±0.433	<0.001	1.000	0.232±0.020	<0.001	1.000	--	--	--
Region West Coast: River Length	-1.037±0.255	<0.001	1.000	-0.053±0.114	<0.001	1.000	--	--	--
River Length: Winter Rain	-0.063±0.084	0.454	0.490	-0.014±0.004	<0.001	1.000	--	--	--
River Length: I(Winter Rain^2)	-0.015±0.040	0.697	0.220	-0.002±0.003	0.360	0.630	--	--	--
River Length:Summer Rain	--	--	--	--	--	--	--	--	--
River Length: I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Mean Gradient:Winter Rain	0.078±0.073	0.283	0.690	0.007±0.003	0.028	1.000	--	--	--
Mean Gradient:I(Winter Rain^2)	-0.075±0.059	0.204	0.780	-0.005±0.002	0.037	1.000	--	--	--
Mean Gradient:Summer Rain	--	--	--	--	--	--	--	--	--
Mean Gradient:I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Prop Lochs:Winter Rain	--	--	--	-0.004±0.004	0.330	0.670	--	--	--
PropLochs:I(WinterRain^2)	--	--	--	0.001±0.001	0.929	0.040	--	--	--
Prop Lochs:Summer Rain	--	--	--	--	--	--	--	--	--
Prop Lochs:I(Summer Rain^2)	--	--	--	--	--	--	--	--	--

A1.4 Time Period 2000 (1990-2000)

A1.4.1 Sea trout catch

River length and Region

A significant interaction between river length and Region highlighted regional differences in sea trout catch in Time Period 2000, indicating that for similar river lengths there were statistically different numbers of sea trout caught in different Regions. This difference in sea trout catch was greater for longer river lengths. A significant interaction between river length and Region was typified by a significant positive relationship between sea trout catch and river length in five Regions (Clyde Coast ($P < 0.001$), Moray Firth ($P = 0.029$), North West ($P < 0.001$), Outer Hebrides ($P = 0.019$), and Solway ($P < 0.001$) (Table A1.9)). All other Regions (East, North, North East, and West) showed no a significant relationship between sea trout catch and river length. As river length declined, the strength of the effect of the interaction decreased. The Importance Value assigned to this interaction by the model dredging process was 1.00 (see Methods for description).

Polynomial of winter rainfall

The relationship between sea trout catch and the second order polynomial term of mean winter rainfall was typified by a significant relationship in Time Period 2000 ($P = 0.002$) (Table A1.9). Predicted sea trout catches declined as winter rainfall increased to a monthly mean of 150mm, but showed a slight increase again when rainfall reached a monthly mean of over 200mm. Mean winter rainfall values ranged from 57.48mm to 214.27mm in Time Period 2000. This Time Period reported the highest mean winter rainfall values of the time series at 155.20 ±1.67 (mean ± SE), indicating that heavy flooding during winter periods could have had detrimental effects on sea trout catches (Table A1.7). The Importance Value assigned to this model term by the model dredging process was 1.00.

Polynomial of winter NAO

Sea trout catch was significantly negatively correlated to the polynomial of mean winter NAO (North Atlantic Oscillation Index) ($P = 0.006$) (Tables A1.1 & A1.9). For example, a slightly higher predicted sea trout catch was reported when winter NAO values were between -0.5 and 0.5, but declined as those values increased or decreased. Mean winter NAO values ranged between -1.80 and 1.59 during Time Period 2000 (Table A1.7). This Time Period reported the highest mean winter NAO value of the time series at 0.42 ± 0.03 (mean ±SE), indicating that climatic events were more extreme and temperatures milder

relative to other Time Periods. The Importance Value assigned to this model term by the model dredging process was 1.00.

Summer NAO

Sea trout catch was significantly negatively correlated to mean summer NAO (P=0.005) (Table A1.9), indicating that as summer NAO values increased, sea trout catch declined. Mean summer NAO values ranged from -1.56 to 1.06 in Time Period 2000 (Table A1.7). The Importance Value assigned to this model term by the model dredging process was 1.00.

Peatland dominance

The percentage of peatland within a District's catchment area had a significant positive relationship with sea trout catch in Time Period 2000 (P- value <0.001) (Table A1.9), indicating that as peatland dominance within a District increased, sea trout catch also increased. Peatland dominance within a District's catchment ranged from 0 to 85.97% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Calcareous geology

The percentage of calcareous geology within a District's catchment area had a significant positive relationship with sea trout catch in Time Period 2000 (P = 0.018) (Table A1.9), indicating that as the percentage of calcareous geology increased, sea trout catch also increased. The percentage of calcareous geology within a District's catchment ranged from 0 to 61.82% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Percent of solid geology

The percentage of solid geology within a District's catchment area had a significantly negative relationship with sea trout catch in Time Period 2000 (P= 0.033) (Table A1.9), indicating that as the percentage of solid geology within a District increased, sea trout catch decreased. The percentage of solid geology within a District's catchment ranged from 7.02 to 87.69% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Mean river gradient

The relationship between the mean river gradient of a District and sea trout catch was typified by a significantly positive relationship in Time Period 2000 (P <0.001) (Table A1.9), indicating that as mean river gradient increased, sea trout catch also increased. Mean river gradient values ranged from 1.97 to 37.92 (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Combined sewer overflows (CSO's)

The relationship between the number of CSO's per kilometre in a District and sea trout catch was typified by a significant positive relationship (P=0.009) (Table A1.9), indicating that as the number of CSO's per kilometre increased, sea trout catch also increased. The Importance Value assigned to this model term by the model dredging process was 1.00.

A1.4.2 Proportional abundance

River length and Region

A significant interaction between river length and Region highlighted regional differences in proportional abundance of sea trout in Time Period 2000, indicating that for similar river lengths there was a statistically different proportional abundance of sea trout caught in different Regions. This difference in proportional abundance was greater for longer river lengths. A significant interaction between river length and Region was typified by a significant positive relationship between proportional abundance and river length in four Regions (Clyde Coast (P <0.001), Moray Firth (P <0.001), North West (P <0.001), Outer Hebrides (P =0.001) and Solway (P <0.001) (Table A1.9). As river length declined, the strength of the effect of the interaction decreased. All other Regions (East, North, North East and West) did not show a significant relationship between proportional abundance and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00.

River length and winter rainfall

An interaction between District river length and mean winter rainfall was typified by a significant relationship between proportional abundance and mean winter rainfall in Time Period 2000 (P <0.001) (Table A1.9). For example, a higher proportional abundance of sea trout was caught in longer rivers when winter rainfall was higher. When winter rainfall remined high in smaller rivers, significantly lower proportions of sea trout were reported. In these same smaller rivers, higher proportional abundance was reported as winter rainfall levels declined. Mean winter rainfall values ranged from 57.48mm to 214.27mm in Time

Period 2000 (Table A1.7). This Time Period reported the highest mean winter rainfall values of the time series at 155.20 ±1.67 (mean ± SE). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Coast

In Time Period 2000, Coast had a significant negative relationship with proportional abundance (P <0.001) (Table A1.9). For example, the proportional abundance of sea trout in the West Coast was significantly lower than the proportional abundance of the East Coast. The Importance Value assigned to this model term by the model dredging process was 1.00.

Polynomial of sea temperature

The polynomial of mean sea temperature was significantly correlated with proportional abundance in Time Period 2000 (P =0.032) (Table A1.9). For example, a higher predicted proportional abundance was reported during this Time Period when sea temperatures were lower, around 9.5°C, and began to decline as temperatures increased, however a slight increase in proportional abundance was observed after temperatures reached 11.0°C. Mean sea temperatures ranged from 9.49°C to 11.76°C in Time Period 2000 (Table A1.7). The Importance Value assigned to this model term by the model dredging process was 1.00.

Percent of solid geology

The percentage of solid geology within a District's catchment area was negatively correlated with proportional abundance in Time Period 2000 (P =0.031) (Table A1.9), indicating that as the percentage of solid geology within a District increased, proportional abundance of sea trout decreased. The percentage of solid geology within a District's catchment ranged from 7.02 to 87.69% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Combined sewer overflows (CSO's)

In Time Period 2000, the number of CSO's per kilometre was significantly positively correlated with proportional abundance (P <0.001) (Table A1.9), indicating that as the number of CSO's per kilometre increased, the proportional abundance of sea trout also increased. The number of CSO's per kilometre within a District ranged from 0.00 to 0.35 (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Mean river gradient and polynomial of winter rainfall

An interaction between the mean river gradient of a District and the second order polynomial term of mean winter rainfall (mm) was typified by a borderline significantly negative relationship in Time Period 2000 (P= 0.057) (Table A1.9). For example, a significantly higher proportional abundance of sea trout was reported in Districts with a lower mean gradient when winter rainfall was high than when rainfall was low. As mean gradient increased, the proportional abundance of sea trout declined regardless of winter rainfall. Mean winter rainfall values ranged from 57.48mm to 214.27mm in Time Period 2000 (Table A1.7). This Time Period reported the highest mean winter rainfall values of the time series at 155.20 ±1.67 (mean ± SE). The Importance Value assigned to this interaction by the model dredging process was 0.94.

A1.4.3 Rate of change

Population variance

A significant positive relationship was found between population variance and rate of change in Time Period 2000 (P =0.033) (Table A1.9), indicating that as the standard deviation of each District's catch rate (as they deviate from the mean of all of Districts combined) increased, so did the rate of change of sea trout catch. Population variance values ranged from 4.76 to 1392.94 in Time Period 2000. The Importance Value assigned to this model term by the model dredging process was 1.00.

Table A1.9.1 - Time Period 2000 Variable Selection (1990-2000)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P-value	Importance	Est±SE	P-value	Importance	Est±SE	P-value	Importance
Geographic Intercept (Region)	5.453±0.291	<0.001	--	0.098±0.016	<0.001	--	0.525±0.784	0.506	--
Coast	-0.157±0.268	0.558	0.430	-0.031±0.015	0.044	only 1 model	-0.772±0.835	0.359	only 1model
River Specific Intercept	5.825±0.047	<0.001	--	0.096±0.002	<0.001	--	-0.050±0.115	0.672	--
Calcareous	0.154±0.052	0.003	1.000		dropped			dropped	
Main River Length	0.667±0.056	<0.001	1.000	0.039±0.003	<0.001	1.000	0.011±0.052	0.828	0.109
Maximum Altitude	0.013±0.040	0.755	0.200	0.007±0.004	0.037	1.000	-0.006±0.041	0.877	0.090
Peat	-0.126±0.053	0.017	1.000	-0.003±0.004	0.301	0.670	-0.28±0.079	0.732	0.213
Solid Geology	-0.345±0.049	<0.001	1.000	-0.012±0.003	<0.001	1.000	-0.013±0.053	0.808	0.119
Mean River Gradient	-0.459±0.059	<0.001	1.000	-0.017±0.004	<0.001	1.000	-0.044±0.099	0.663	0.259
CSO/km	-0.202±0.053	<0.001	1.000	-0.007±0.003	0.007	1.000	0.009±0.045	0.846	0.101
Flood10	0.010±0.030	0.728	0.220	0.008±0.003	0.014	1.000		dropped	
Prop Lochs	0.008±0.029	0.788	0.190	-0.014±0.004	<0.001	1.000		dropped	
Climatic Intercept	5.288±0.094	<0.001	--	0.061±0.005	<0.001	--	-0.772±0.835	0.359	--
Sea Temperature	-0.005±0.031	0.867	0.270	-0.004±0.003	0.195	0.800	-0.010 ±0.053	0.849	0.169
I(Sea Temperature^2)	0.277±0.043	<0.001	1.000	0.013±0.002	<0.001	1.000	0.012±0.057	0.844	0.171
Air Temperature		co-correlated			co-correlated			co-correlated	
I(Air Temperature^2)		co-correlated			co-correlated			co-correlated	
Mean Winter Rain	-0.255±0.063	<0.001	1.000	-0.022±0.003	<0.001	1.00	-0.022±0.069	0.755	0.215
I(Mean Winter Rain^2)	0.369±0.048	<0.001	1.000	0.025±0.003	<0.001	1.00		dropped	
Mean Summer Rain		co-correlated			co-correlated			co-correlated	
I(Mean Summer Rain^2)		co-correlated			co-correlated			co-correlated	
Winter NAO		dropped		0.000±0.002	0.859	0.18		co-correlated	

Table A1.9.1 (continued) - Time Period 2000 Variable Selection (1990-2000)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P-value	Importance	Est±SE	P-value	Importance	Est±SE	P-value	Importance
I(Winter NAO^2)	-0.085±0.035	0.015	1.000	-0.003±0.002	0.042	1.00		co-correlated	
Summer NAO	-0.145±0.055	0.008	1.000	-0.000±0.001	0.896	0.17		co-correlated	
I(Summer NAO^2)		co-correlated			co-correlated			co-correlated	

Table A1.9.2 - Time Period 2000 Averaged Model (1990-2000)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Intercept (Clyde Coast)	4.545±0.264	<0.001	1.000	0.080±0.022	<0.001	1.000	--	--	--
Region East	0.939±0.491	0.059	1.000	0.029±0.029	0.312	1.000	--	--	--
Region Moray Firth	0.851±0.286	0.003	1.000	-0.002±0.022	0.919	1.000	--	--	--
Region North	1.076±0.364	0.003	1.000	0.020±0.021	0.345	1.000	--	--	--
Region North East	1.541±0.419	<0.001	1.000	0.062±0.026	0.018	1.000	--	--	--
Region North West	3.080±0.436	<0.001	1.000	0.134±0.019	<0.001	1.000	--	--	--
Region Outer Hebrides	2.687±0.454	<0.001	1.000	0.147±0.020	<0.001	1.000	--	--	--
Region Solway	2.108±0.282	<0.001	1.000	0.132±0.012	<0.001	1.000	--	--	--
Region West Coast	-0.290±0.321	0.367	1.000	0.012±0.013	0.304	1.000	--	--	--
Coast	--	--	--	-0.051±0.018	0.006	1.000	--	--	--
Calcareous	0.121±0.051	0.018	1.000	--	--	--	--	--	--
River Length	-0.739±0.559	0.187	1.000	-0.052±0.023	0.027	1.000	--	--	--
Altitude	--	--	--	0.001±0.001	0.913	0.060	--	--	--
Peat	0.236±0.055	<0.001	1.000	--	--	--	--	--	--
Solid Geology	-0.090±0.042	0.033	1.000	-0.003±0.002	0.040	1.000	--	--	--

Table A1.9.2 (continued) - Time Period 2000 Averaged Model (1990-2000)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
CSO/km	0.461±0.176	0.009	1.000	0.029±0.007	<0.001	1.000	--	--	--
Mean River Gradient	0.280±0.068	<0.001	1.000	0.005±0.003	0.078	0.940	--	--	--
Flood10	--	--	--	-0.001±0.002	0.601	0.320	--	--	--
Proportion Lochs	--	--	--	-0.001±0.002	0.735	0.200	--	--	--
Sea Temperature	-0.002±0.019	0.918	0.050	-0.001±0.001	0.942	0.030	--	--	--
I(Sea Temperature^2)	0.049±0.047	0.294	0.710	0.004±0.002	0.032	1.000	--	--	--
Air Temperature	--	--	--	--	--	--	--	--	--
I(Air Temperature^2)	--	--	--	--	--	--	--	--	--
Winter Rain	-0.256±0.075	0.001	1.000	-0.014±0.004	<0.001	1.000	--	--	--
I(Winter Rain^2)	0.219±0.069	0.002	1.000	0.008±0.003	0.017	1.000	--	--	--
Summer Rain	--	--	--	--	--	--	--	--	--
I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Winter NAO	-0.002±0.015	0.916	0.050	0.001±0.002	0.538	0.410	--	--	--
I(Winter NAO^2)	-0.080±0.029	0.006	1.000	-0.001±0.001	0.532	0.420	--	--	--
Summer NAO	-0.118±0.042	0.005	1.000	--	--	--	--	--	--
I(Summer NAO^2)	--	--	--	--	--	--	--	--	--
Population Variance	--	--	--	--	--	--	0.315±0.144	0.032	only 1 model
Region East: Main River	0.827±0.581	0.155	1.000	0.028±0.025	0.256	1.000	--	--	--
Region Moray Firth: River Length	1.335±0.611	0.029	1.000	0.098±0.026	<0.001	1.000	--	--	--
Region North: River Length	0.231±0.742	0.756	1.000	0.014±0.040	0.731	1.000	--	--	--
Region North East: River Length	0.243±0.492	0.622	1.000	-0.012±0.021	0.566	1.000	--	--	--
Region North West: River Length	6.886±0.801	<0.001	1.000	0.264±0.035	<0.001	1.000	--	--	--
Region Outer Hebrides:River Length	1.961±0.834	0.019	1.000	0.118±0.035	0.001	1.000	--	--	--
Region Solway: Main River	4.253±0.692	<0.001	1.000	0.282±0.029	<0.001	1.000	--	--	--

Table A1.9.2 (continued) - Time Period 2000 Averaged Model (1990-2000)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Region West Coast: River Length	0.066±0.598	0.913	1.000	0.043±0.024	0.087	1.000	--	--	--
River Length: Winter Rain	-0.019±0.050	0.695	0.250	-0.016±0.003	<0.001	1.000	--	--	--
River Length: I(Winter Rain^2)		dropped			dropped		--	--	--
River Length:Summer Rain	--	--	--	--	--	--	--	--	--
River Length: I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Mean Gradient:Winter Rain	0.020±0.044	0.649	0.290	0.001±0.001	0.789	0.180	--	--	--
Mean Gradient:I(Winter Rain^2)	-0.058±0.058	0.317	0.680	-0.005±0.002	0.057	0.940	--	--	--
Mean Gradient:Summer Rain	--	--	--	--	--	--	--	--	--
Mean Gradient:I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Prop Lochs:Winter Rain	--	--	--	0.001±0.001	0.801	0.090	--	--	--
PropLochs:I(WinterRain^2)	--	--	--		dropped		--	--	--
Prop Lochs:Summer Rain	--	--	--	--	--	--	--	--	--
Prop Lochs:I(Summer Rain^2)	--	--	--	--	--	--	--	--	--

A1.5 Time Period 2008 (2000-2008)

A1.5.1 Sea trout catch

River length and Region

A significant interaction between river length and Region highlighted regional differences in sea trout catch in Time Period 2008, indicating that for similar river lengths there were statistically different numbers of sea trout caught in different Regions. This difference in sea trout catch was greater for longer river lengths. Three Regions (Clyde Coast, Solway, and North West) had a significant positive relationship between sea trout catch and river length ($P < 0.001$), while five Regions (East, Moray Firth, North, North East and West Coast ($P < 0.001$) (Table A1.10)) all had a significant negative relationship between sea trout catch and river length. A District with a long river length in the Solway Region reported a significantly higher sea trout catch comparted to a District with a similar river length in the North Region. As river length declined, the strength of the effect of the interaction decreased.

All other Regions (Outer Hebrides) showed no significant relationship between sea trout catch and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00 (see Methods for description).

River length and winter rainfall

An interaction between river length and mean winter rainfall was typified by a significant negative relationship in Time Period 2008 ($P = 0.002$) (Table A1.10). For example, the highest sea trout catches were reported in longer rivers when the mean monthly winter rainfall was below 100mm. Significantly lower sea trout catches were reported in shorter rivers that received the same amount of winter rainfall. As mean rainfall increased, sea trout catch across all rivers declined. Mean winter rainfall values ranged from 61.42mm to 221.22mm in Time Period 2008 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Mean river gradient and summer rainfall

In Time Period 2008, an interaction between the mean river gradient of a District and mean summer rainfall was typified by a significant positive relationship with sea trout catch ($P < 0.001$) (Table A1.10). For example, Districts with low mean gradients saw the highest predicted sea trout catch during periods of low monthly mean rainfall, between 40 and 60 mm per month. However, sea trout catches declined in these same Districts as monthly

summer rainfall increased. Districts with a higher mean gradient reported lower predicted sea trout catches than those with lower gradients, but their numbers also declined as mean summer rainfall increased. Mean summer rainfall values ranged from 39.17mm to 124.78mm in Time Period 2008 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Polynomial of winter NAO

Sea trout catch was significantly correlated to the polynomial of mean winter NAO (P=0.025) (Table A1.10) in Time Period 2008. Sea trout catch initially increased with winter NAO values, but began a slight decline after NAO values reached 1.0. Mean winter NAO values ranged from -0.79 to 1.21 in Time Period 2008 (Table A1.7). The Importance Value assigned to this model term by the model dredging process was 1.00.

Summer rainfall

In Time Period 2008, mean monthly summer rainfall was positively correlated with sea trout catch (P =0.002) (Table A1.10), indicating that as summer rainfall increased, so did sea trout catch. Mean summer rainfall values ranged from 39.17mm to 124.78mm in Time Period 2008 (Table A1.7). The Importance Value assigned to this model term by the model dredging process was 1.00.

Peatland dominance

In Time Period 2008, the percentage of peatland within a District's catchment area had a significantly positive relationship with sea trout catch (P= 0.039) (Table A1.10), indicating that as peatland dominance increased, sea trout catch also increased. Peatland dominance within a District's catchment ranged from 0 to 85.97% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Percentage of solid geology

The percentage of solid geology within a District's catchment area was typified by a negative relationship with sea trout catch in Time Period 2008 (P <0.001) (Table A1.10), indicating that as the percentage of solid geology increased, sea trout catch declined. The percentage of solid geology within a District's catchment ranged from 7.02 to 87.69% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

A1.5.2 Proportional abundance

River length and Region

A significant interaction between river length and Region highlighted regional differences in proportional abundance in Time Period 2008, indicating that there was a statistically different proportional abundance of sea trout caught in different Regions. Three Regions (Clyde Coast, Solway, and North West) had a significant positive relationship between proportional abundance and river length ($P < 0.001$), while five Regions (East, Moray Firth, North, North East and West Coast ($P < .001$) (Table A1.10)) had a significant negative relationship between proportional abundance and river length. A District with a long river length in the Solway Region reported a significantly higher proportional abundance compared to a District with a similar river length in the North Region. As river length declined, the strength of the effect of the interaction decreased. The Outer Hebrides Region showed no significant relationship between proportional abundance and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00.

River length and winter rainfall

A significant interaction between mean winter rainfall and river length was typified by a negative relationship between proportional abundance and river length in Time Period 2008 ($P < 0.001$) (Table A1.10). For example, a higher proportional abundance of sea trout was reported from longer rivers when mean winter rainfall was low, however as rainfall increased in these rivers, the proportion declined. There was a significantly lower proportional abundance of sea trout reported in smaller rivers, but this proportion declined as winter rainfall increased. Mean winter rainfall values ranged from 61.42mm to 221.22mm in Time Period 2008 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

River length and polynomial of summer rainfall

In Time Period 2008, a significant interaction between District river length and the polynomial of mean summer rainfall was typified by a significant relationship between proportional abundance and river length ($P = 0.019$) (Table A1.10). For example, significantly higher proportional abundance was reported in longer rivers with lower mean monthly summer rainfall than was reported in smaller rivers with similar rainfall levels. All rivers saw a decline in their predicted proportional abundance as summer rainfall increased, however a greater decline was observed in longer rivers, rather than smaller rivers. Mean summer rainfall values ranged from 39.17mm to 124.78mm in Time Period

2008 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Percentage of lochs and summer rainfall

A significant interaction between the percentage of lochs within a District's catchment area and mean summer rainfall was typified by a significant positive relationship between proportional abundance of sea trout and mean summer rainfall in Time Period 2008 (P = 0.013) (Table A1.10). Districts with a higher percentage of lochs within their catchments saw significantly higher proportions of sea trout captured when mean monthly summer rainfall was highest than when rainfall levels dropped. Districts with a lower percentage of lochs saw higher proportions of sea trout reported when summer rainfall was at its lowest, with the proportional abundance of sea trout falling as summer rainfall levels increased. Mean summer rainfall values ranged from 39.17mm to 124.78mm in Time Period 2008 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Mean river gradient

Proportional abundance was significantly positively correlated with the mean gradient of a District in Time Period 2008 (P= 0.002) (Table A1.10), indicating that as the mean gradient of a river increased, proportional abundance of sea trout also increased. Mean river gradient values ranged from 1.97 to 37.92 (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Percentage of solid geology

The percentage of solid geology within a District's catchment area had a significant negative relationship with proportional abundance in Time Period 2008 (P =0.003) (Table A1.10), indicating that as the percentage of solid geology increases, proportional abundance declined. The percentage of solid geology within a District's catchment ranged from 7.02 to 87.69% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

A1.5.3 Rate of change

Population variance

A significant negative relationship was found between population variance and rate of change in Time Period 2008 (P = 0.001) (Table A1.10), indicating that as the standard

deviation of each District's catch rate (as they deviate from the mean of all of Districts combined) increased, so did the rate of change of sea trout catch. Population variance values ranged from 10.39 to 1217.20 in Time Period 2008. The Importance Value assigned to this model term by the model dredging process was 1.00.

Polynomial of sea temperature

A significant negative relationship was found between the polynomial of sea temperature (C°) and rate of change in Time Period 2008 (P = 0.035) (Table A1.10). For example, the predicted rate of change increases to a value of 0.50 as sea temperatures reach an estimated 11°C, indicating that sea trout populations are increasing at the quickest rate at this temperature. However, once temperatures reach an estimated 11.2°C, the predicted rate of change begins to decline and reaches a value of -0.50 at around 12°C, indicating that sea trout populations are declining at a faster rate. Mean sea temperatures ranged from 10.10°C to 12.13°C in Time Period 2008 (Table A1.7). This Time Period reported the highest mean sea temperatures of the time series at 11.03± 0.02 (mean ± SE). The Importance Value assigned to this model term by the model dredging process was 1.00.

Table A1.10.1 - Time Period 2008 Variable Selection (2000-2008)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P-value	Importance	Est±SE	P-value	Importance	Est±SE	P-value	Importance
Geographic Intercept (Region)	5.525±0.214	<0.001	--	0.070±0.013	<0.001	--	-0.564±0.669	0.405	--
Coast	-0.0280±0.177	0.876	0.270	-0.004±0.011	0.733	0.310	0.321±0.613	0.604	0.360
River Specific Intercept	5.751±0.049	<0.001	--	0.098±0.003	<0.001	--	0.001±0.11	1.000	--
Calcareous	-0.023±0.045	0.612	0.300	-0.007±0.003	0.015	1.000	0.004±0.032	0.907	0.050
Main River Length	0.577±0.056	<0.001	1.000	0.041±0.003	<0.001	1.000	0.246±0.147	0.100	0.880
Maximum Altitude	0.012±0.041	0.770	0.210	0.003±0.004	0.464	0.510	-0.048±0.122	0.693	0.190
Peat	-0.089±0.061	0.146	0.890	-0.003±0.003	0.387	0.590	0.020±0.070	0.774	0.140
Solid Geology	-0.408±0.052	<0.001	1.000	-0.013±0.003	<0.001	1.000		dropped	
Mean River Gradient	-0.339±0.062	<0.001	1.000	-0.010±0.004	0.014	1.000	0.185±0.178	0.304	0.680
CSO/km	-0.002±0.016	0.911	0.090	0.002±0.003	0.513	0.470	-0.034±0.085	0.695	0.250
Flood10	0.002±0.017	0.900	0.090	0.003±0.004	0.450	0.530	-0.005±0.041	0.905	0.050
Prop Lochs	0.001±0.017	0.933	0.080	-0.012±0.004	0.002	1.000	0.193±0.161	0.236	0.760
Climatic Intercept	5.379±0.109	<0.001	--	0.064±0.005	<0.001	--	0.638±0.217	0.004	--
Sea Temperature	-0.099±0.068	0.144	0.880	-0.012±0.003	<0.001	1.000		dropped	
I(Sea Temperature^2)	0.289±0.051	<0.001	1.000	0.012±0.002	<0.001	1.000	-0.438±0.116	<0.001	1.000
Air Temperature	co-correlated	co-correlated	co-correlated	co-correlated	co-correlated	co-correlated	co-correlated	co-correlated	co-correlated
I(Air Temperature^2)	co-correlated	co-correlated	co-correlated	co-correlated	co-correlated	co-correlated	co-correlated	co-correlated	co-correlated
Mean Winter Rain	-0.087±0.097	0.370	0.610	-0.023±0.004	<0.001	1.000	-0.053±0.184	0.774	0.280
I(Mean Winter Rain^2)	0.278±0.055	<0.001	1.000	0.017±0.003	<0.001	1.000	-0.210±0.119	0.084	1.000
Mean Summer Rain	-0.037±0.068	0.585	0.390	-0.001±0.003	0.711	0.220	co-correlated	co-correlated	co-correlated
I(Mean Summer Rain^2)	0.182±0.054	0.001	1.000	0.005±0.003	0.077	0.940	co-correlated	co-correlated	co-correlated

Winter NAO	0.184±0.083	0.026	1.000	0.002±0.004	0.520	0.430	co-correlated	co-correlated	co-correlated

Table A1.10.1 (continued) - Time Period 2008 Variable Selection (2000-2008)

	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P-value	Importance	Est±SE	P-value	Importance	Est±SE	P-value	Importance
I(Winter NAO^2)	-0.349±0.085	<0.001	1.000	-0.001±0.002	0.701	0.230	co-correlated	co-correlated	co-correlated
Summer NAO	0.161±0.066	0.015	1.000	-0.000±0.001	0.836	0.080	co-correlated	co-correlated	co-correlated
I(Summer NAO^2)	0.010±0.038	0.795	0.200	0.002±0.003	0.533	0.420	co-correlated	co-correlated	co-correlated

Table A1.10.2 - Time Period 2008 Averaged Model (2000-2008)

	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Intercept (Clyde Coast)	5.085±0.134	<0.001	1.000	0.077±0.005	<0.001	1.000		dropped	
Region East	1.503±0.475	0.002	1.000	0.077±0.017	<0.001	1.000		dropped	
Region Moray Firth	0.456±0.245	0.064	1.000	0.011±0.009	0.262	1.000		dropped	
Region North	0.420±0.279	0.134	1.000	0.017±0.012	0.147	1.000		dropped	
Region North East	1.766±0.396	<0.001	1.000	0.090±0.012	<0.001	1.000		dropped	
Region North West	1.745±0.354	<0.001	1.000	0.098±0.020	<0.001	1.000		dropped	
Region Outer Hebrides	1.951±0.397	<0.001	1.000	0.120±0.020	<0.001	1.000		dropped	
Region Solway	1.117±0.174	<0.001	1.000	0.054±0.008	<0.001	1.000		dropped	
Region West Coast	-0.641±0.182	<0.001	1.000	-0.020±0.008	0.013	1.000		dropped	
Coast	--	--	--	--		--		dropped	
Calcareous	--	--	--	-0.004±0.003	0.092	0.920		dropped	
River Length	1.204±0.136	<0.001	1.000	0.078±0.007	<0.001	1.000	-0.013±0.058	0.830	0.160
Altitude	--	--	--	--	--	--	--	--	--
Peat	0.118±0.057	0.039	1.000	--	--	--	--	--	--
Solid Geology	-0.205±0.044	<0.001	1.000	-0.006±0.002	0.003	1.000	--	--	--

Table A1.10.2 (continued) - Time Period 2008 Averaged Model (2000-2008)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
CSO/km	--	--	--	--	--	--	--	--	--
Mean River Gradient	0.221±0.062	<0.001	1.000	0.010±0.003	0.002	1.000	--	--	--
Flood10	--	--	--	--	--	--	--	--	--
Proportion Lochs	--	--	--	-0.012±0.003	0.001	1.000	--	--	--
Sea Temperature	-0.010±0.047	0.829	0.100	0.001±0.001	0.901	0.070		dropped	
I(Sea Temperature^2)		dropped			dropped		-0.330±0.0107	0.002	1.000
Air Temperature	--	--	--	--	--	--	--	--	--
I(Air Temperature^2)	--	--	--	--	--	--	--	--	--
Winter Rain	-0.135±0.106	0.205	1.000	-0.005±0.003	0.072	1.000	0.015±0.059	0.806	0.170
I(Winter Rain^2)	0.071±0.065	0.274	0.740			dropped	-0.017±0.047	0.716	0.230
Summer Rain	0.185±0.060	0.002	1.000	0.002±0.003	0.454	1.000	--	--	--
I(Summer Rain^2)		dropped		-0.003±0.002	0.194	1.000	--	--	--
Winter NAO	0.081±0.067	0.225	0.770	--	--	--	--	--	--
I(Winter NAO^2)	-0.128±0.057	0.025	1.000	--	--	--	--	--	--
Summer NAO	--	--	--	--	--	--	--	--	--
I(Summer NAO^2)	--	--	--	--	--	--	--	--	--
Population Variance	--	--	--	--	--	--	-0.393±0.119	0.001	1.000
Region East: Main River	-1.679±0.233	<0.001	1.000	-0.111±0.010	<0.001	1.000		dropped	
Region Moray Firth: River Length	-0.968±0.206	<0.001	1.000	-0.047±0.010	<0.001	1.000		dropped	
Region North: River Length	-2.177±0.550	<0.001	1.000	-0.078±0.022	<0.001	1.000		dropped	
Region North East: River Length	-1.542±0.303	<0.001	1.000	-0.101±0.014	<0.001	1.000		dropped	
Region North West: River Length	3.203±0.623	<0.001	1.000	0.162±0.036	<0.001	1.000		dropped	

Table A1.10.2 (continued) - Time Period 2008 Averaged Model (2000-2008)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Region Outer Hebrides:River Length	-0.505±0.655	0.441	1.000	-0.001±0.032	0.965	1.000		dropped	
Region Solway: Main River	1.992±0.434	<0.001	1.000	0.113±0.019	<0.001	1.000		dropped	
Region West Coast: River Length	-0.942±0.254	<0.001	1.000	-0.062±0.012	<0.001	1.000		dropped	
River Length: Winter Rain	-0.251±0.082	0.002	1.000	-0.019±0.003	<0.001	1.000	--	--	--
River Length: I(Winter Rain^2)	-0.004±0.020	0.823	0.100		dropped			dropped	
River Length:Summer Rain	-0.112±0.067	0.096	1.000	-0.016±0.004	<0.001	1.000	--	--	--
River Length: I(Summer Rain^2)		dropped		-0.003±0.001	0.019	1.000	--	--	--
Mean Gradient:Winter Rain		dropped			dropped		--	--	--
Mean Gradient:I(Winter Rain^2)	-0.004±0.016	0.813	0.110		dropped		--	--	--
Mean Gradient:Summer Rain	0.203±0.053	<0.001	1.000	0003±0.003	0.325	0.670	--	--	--
Mean Gradient:I(Summer Rain^2)		dropped		-0.002±0.002	0.333	0.660	--	--	--
Prop Lochs:Winter Rain	--	--	--		dropped		--	--	--
PropLochs:I(WinterRain^2)	--	--	--		dropped		--	--	--
Prop Lochs:Summer Rain	--	--	--	0.008±0.003	0.013	1.000	--	--	--
Prop Lochs:I(Summer Rain^2)	--	--	--	-0.002±0.003	0.495	0.460	--	--	--

A1.6 Time Period 2014 (2008-2014)

A1.6.1 Sea trout catch

River length and Region

A significant interaction between river length and Region highlighted regional differences in sea trout catch in Time Period 2014, indicating that for similar river lengths, there were statistically different numbers of sea trout caught in different Regions. This difference in sea trout catch was greater for longer river lengths. The Clyde Coast, Solway and North West Region all had a significantly positive relationship between sea trout catch and river length ($P < 0.001$) (Table A1.11). Three Regions (East, Moray Firth and North East) had a significantly negative relationship between sea trout catch and river length ($P < 0.001$). A District with a long river length in the North West Region reported significantly higher sea trout catches compared to similarly sized rivers in the North East Region. As river length declined, the strength of the effect of the interaction decreased. All other Regions (West Coast, Outer Hebrides and North) showed no significant relationship between sea trout catch and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00 (see Methods for description).

River length and winter rainfall

The interaction between river length and mean winter rainfall was typified by a significant relationship in Time Period 2014 ($P = 0.011$) (Table A1.11). The highest sea trout catches were reported in longer rivers when the mean monthly winter rainfall was below 100mm. Significantly lower sea trout catches were reported in smaller rivers that received the same amount of winter rainfall. As mean winter rainfall increased, sea trout catch across all rivers declined. Mean winter rainfall values ranged from 50.63mm to 211.57mm in Time Period 2014 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Mean river gradient and polynomial of winter rainfall

In Time Period 2014, an interaction between mean river gradient of a District and the second order polynomial term of mean winter rainfall was typified by a significant positive relationship between sea trout catch and mean gradient ($P = 0.004$) (Table A1.11). For example, Districts with a lower mean gradient observed the highest sea trout catches when monthly mean winter rainfall levels were low, but catches decreased as rainfall increased. Districts with a high mean gradient also saw higher sea trout catches during periods of

lower winter rainfall, but their catches were smaller than those with lower mean gradients, and declined as winter rainfall increased. As mean winter rainfall increased, sea trout catch across all rivers declined. Mean winter rainfall values ranged from 50.63mm to 211.57mm in Time Period 2014 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

A1.6.2 Proportional abundance

River length and Region

A significant interaction between river length and Region highlighted regional differences in proportional abundance of sea trout in Time Period 2014, indicating that for similar river length there was a statistically different proportional abundance of sea trout caught in different Regions. This difference in proportional abundance was greater for longer river lengths. Four Regions (Clyde Coast ($P < 0.001$), Outer Hebrides ($P = 0.001$), Solway ($P < 0.001$), and North West ($P < 0.001$) (Table A1.11)) had a significant positive relationship between proportional abundance and river length, while five Regions (East ($P < 0.001$), Moray Firth ($P = 0.001$), North ($P = 0.040$), North East ($P < 0.001$) and West Coast ($P < 0.001$)) had a significant negative relationship between proportional abundance and river length. A District with a long river length in the Solway Region reported a higher proportional abundance compared to a District with a similar river length in the West Coast Region. As river length declined, the strength of the effect of the interaction decreased. The Importance Value assigned to this interaction by the model dredging process was 1.00.

River length and polynomial of winter rainfall

The relationship between the polynomial of mean winter rainfall and river length was typified by a significant interaction between proportional abundance and the polynomial winter rainfall in Time Period 2014 ($P = 0.016$) (Table A1.11). A higher predicted proportional abundance of sea trout was reported from longer rivers when mean winter rainfall is low, however as rainfall increases in these rivers, the proportional abundance of sea trout declines. There is a significantly lower proportional abundance of sea trout reported in smaller rivers, but this proportional abundance also drops as winter rainfall increases. Mean winter rainfall values ranged from 50.63mm to 211.57mm in Time Period 2014 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Mean river gradient and polynomial of winter rainfall

In Time Period 2014, a significant interaction between mean river gradient of a District and the polynomial of mean winter rainfall was typified by a significant relationship between proportional abundance and winter rainfall (P <0.001) (Table A1.11). For example, a higher proportional abundance of sea trout was reported in Districts with a lower mean gradient during periods of low winter rainfall. As rainfall increased in these Districts, proportional abundance declined. Districts with higher mean gradients reported similar trends of proportional abundance decline with increased rainfall, however an overall lower proportion was reported in these Districts than was found in Districts with lower gradients. Mean winter rainfall values ranged from 50.63mm to 211.57mm in Time Period 2014 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Percentage of lochs

A significant negative relationship between the percentage of lochs within a District's catchment area and proportional abundance was demonstrated in Time Period (P <0.001) (Table A1.11), indicating that as the percentage of lochs within a District increased, proportional abundance of sea trout decreased. The percentage of a District comprised of lochs ranged from 0.00 to 43.49% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Calcareous geology

The percentage of calcareous geology within a District's catchment area had a significantly negative relationship with proportional abundance in Time Period 2014 (P=0.037) (Table A1.11), indicating that as the percent of calcareous geology increased, proportional abundance declined. The percentage of calcareous geology within a District's catchment ranged from 0 to 61.82% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Peatland dominance

The percentage of peatland within a District's catchment area was significantly positively correlated with proportional abundance in Time Period 2014 (P <0.001) (Table A1.11), indicating that as peatland dominance increased, proportional abundance also increased. Peatland dominance within a District's catchment ranged from 0 to 85.97% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

A1.6.3 Rate of change

Peatland dominance

A significant positive relationship was found between the percentage of peatland in a District's catchment area and rate of change Time period 2014 (P = 0.046) (Table A1.11), indicating that as peatland dominance increased, a District's rate of change increased. Peatland dominance within a District's catchment ranged from 0 to 85.97% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Table A1.11.1 - Time Period 2014 Variable Selection (2008-2014)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P-value	Importance	Est±SE	P-value	Importance	Est±SE	P-value	Importance
Geographic Intercept (Region)	5.276±0.0349	<0.001	--	0.097±0.018	<0.001	--	0.041±0.124	0.748	--
Coast	-0.225±0.327	0.492	0.49	-0.034±0.017	0.038	only 1 model	0.049±0.127	0.702	0.32
River Specific Intercept	5.772±0.053	<0.001	--	0.102±0.003	<0.001	--	0.075±0.078	0.344	--
Calcareous	-0.047±0.062	0.449	0.51	-0.007±0.003	0.023	1.00		dropped	
Main River Length	0.529±0.059	<0.001	1.00	0.040±0.003	<0.001	1.00		dropped	
Maximum Altitude	0.002±0.022	0.914	0.06	0.000±0.002	0.882	0.11		dropped	
Peat	0.029±0.052	0.579	0.4	0.007±0.003	0.031	1.00	0.160±0.077	0.041	1.00
Solid Geology	-0.186±0.055	0.001	1.00	-0.007±0.003	0.015	1.00	0.011±0.042	0.798	0.22
Mean River Gradient	-0.296±0.062	<0.001	1.00	-0.005±0.004	0.215	0.81		dropped	
CSO/km	-0.044±0.061	0.466	0.5	-0.001±0.002	0.75	0.17		dropped	
Flood10		dropped		0.000±0.002	0.829	0.13	-0.010±0.041	0.807	0.22
Prop Lochs	0.002±0.018	0.891	0.06	-0.007±0.004	0.105	0.89		dropped	
Climatic Intercept	6.131±0.298	<0.001	--	0.093±0.018	<0.001	--	0.089±0.086	0.305	--
Sea Temperature	-0.046±0.080	0.565	0.37	-0.017±0.004	<0.001	1.00		dropped	
I(Sea Temperature^2)	0.0118±0.047	0.012	1.00	0.006±0.002	0.018	1.00		dropped	
Air Temperature	-0.403±0.114	<0.001	1.00	-0.001±0.003	0.85	0.17		co-correlated	
I(Air Temperature^2)		dropped		-0.001±0.002	0.53	0.41		co-correlated	
Mean Winter Rain	-0.154±0.106	0.145	0.82	-0.015±0.006	0.02	0.96	0.029±0.065	0.656	0.288
I(Mean Winter Rain^2)	0.277±0.063	<0.001	1.00	0.018±0.004	<0.001	1.00	-0.016±0.036	0.658	0.286
Mean Summer Rain	-0.008±0.038	0.842	0.16	-0.001±0.003	0.741	0.18		co-correlated	
I(Mean Summer Rain^2)	0.059±0.067	0.376	0.58	0.002±0.003	0.491	0.47		co-correlated	
Winter NAO	-08.009±0.036	0.806	0.09	-0.002±0.004	0.619	0.3		co-correlated	

Table A1.11.1 (continued) - Time Period 2014 Variable Selection (2008-2014)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P-value	Importance	Est±SE	P-value	Importance	Est±SE	P-value	Importance
I(Winter NAO^2)	-0.402±0.176	0.023	1.00	-0.007±0.010	0.445	0.47	co-correlated		
Summer NAO	0.479±0.144	0.001	1.00	0.007±0.008	0.394	0.56	co-correlated		
I(Summer NAO^2)	-0.437±0.100	<0.001	1.00	-0.008±0.005	0.114	0.93	co-correlated		

Table A1.11.2 - Time Period 2014 Averaged Model (2008-2014)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Intercept (Clyde Coast)	4.787±0.177	<0.001	1.00	0.077±0.010	<0.001	1.00	--	--	--
Region East	1.708±0.474	<0.001	1.00	0.102±0.022	<0.001	1.00	--	--	--
Region Moray Firth	0.476±0.296	0.108	1.00	-0.008±0.013	0.53	1.00	--	--	--
Region North	1.735±0.309	<0.001	1.00	0.052±0.014	<0.001	1.00	--	--	--
Region North East	1.594±0.388	<0.001	1.00	0.082±0.018	<0.001	1.00	--	--	--
Region North West	1.552±0.371	<0.001	1.00	0.125±0.020	<0.001	1.00	--	--	--
Region Outer Hebrides	2.550±0.429	<0.001	1.00	0.200±0.019	<0.001	1.00	--	--	--
Region Solway	1.036±0.178	<0.001	1.00	0.045±0.008	<0.001	1.00	--	--	--
Region West Coast	-0.128±0.202	0.526	1.00	-0.004±0.008	0.598	1.00	--	--	--
Coast	--	--	--	-0.002±0.008	0.854	0.13	--	--	--
Calcareous	--	--	--	-0.005±0.002	0.037	1.00	--	--	--
River Length	1.144±0.139	<0.001	1.00	0.062±0.007	<0.001	1.00	--	--	--
Altitude	--	--	--	--	--	--	--	--	--
Peat	--	--	--	0.015±0.003	<0.001	1.00	0.156±0.076	0.046	1.00
Solid Geology		dropped		0.001±0.001	0.848	0.13	--	--	--
CSO/km	--	--	--	--	--	--	--	--	--

Table A1.11.2 (continued) - Time Period 2014 Averaged Model (2008-2014)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
CSO/km	--	--	--	--	--	--	--	--	--
Mean River Gradient	0.296±0.062	<0.001	1.00	0.027±0.004	<0.001	1.00	--	--	--
Flood10	--	--	--	--	--	--	--	--	--
Proportion Lochs	--	--	--	-0.017±0.004	<0.001	1.00	--	--	--
Sea Temperature	0.046±0.085	0.59	0.32		dropped		--	--	--
I(Sea Temperature^2)	-0.006±0.022	0.787	0.14		dropped		--	--	--
Air Temperature	0.008±0.0297	0.797	0.1	--	--	--	--	--	--
I(Air Temperature^2)	--	--	--	--	--	--	--	--	--
Winter Rain	-0.092±0.084	0.278	1.00	0.001±0.004	0.708	1.00	--	--	--
I(Winter Rain^2)	0.068±0.069	0.324	1.00	-0.002±0.003	0.635	1.00	--	--	--
Summer Rain	--	--	--	--	--	--	--	--	--
I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Winter NAO	-0.025±0.050	0.622	0.32	--	--	--	--	--	--
I(Winter NAO^2)	0.008±0.033	0.807	0.12	--	--	--	--	--	--
Summer NAO	0.013±0.036	0.725	0.19	dropped	--	--	--		
I(Summer NAO^2)	-0.021±0.039	0.6	0.3	dropped	--	--	--		
Population Variance	--	--	--	--	--	--	0.046±0.088	0.603	0.38
Region East: Main River	-1.360±0.225	<0.001	1.00	-0.082±0.011	<0.001	1.00	--	--	--
Region Moray Firth: River Length	-0.821±0.206	<0.001	1.00	-0.034±0.010	0.001	1.00	--	--	--
Region North: River Length	0.178±0.496	0.72	1.00	-0.058±0.028	0.04	1.00	--	--	--
Region North East: River Length	-1.313±0.301	<0.001	1.00	-0.102±0.014	<0.001	1.00	--	--	--
Region North West: River Length	2.244±0.637	<0.001	1.00	0.228±0.035	<0.001	1.00	--	--	--
Region Outer Hebrides:River Length	-0.619±0.664	0.352	1.00	0.107±0.033	0.001	1.00	--	--	--

Table A1.11.2 (continued) - Time Period 2014 Averaged Model (2008-2014)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Region Solway: Main River	1.578±0.439	<0.001	1.00	0.102±0.019	<0.001	1.00	--	--	--
Region West Coast: River Length	-0.407±0.258	0.116	1.00	-0.044±0.012	<0.001	1.00	--	--	--
River Length: Winter Rain	-0.186±0.072	0.011	1.00	-0.012±0.003	<0.001	1.00	--	--	--
River Length: I(Winter Rain^2)	0.001±0.007	0.945	0.02	0.005±0.002	0.016	1.00	--	--	--
River Length:Summer Rain	--	--	--	--	--	--	--	--	--
River Length: I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Mean Gradient:Winter Rain	0.047±0.061	0.441	0.52	0.007±0.003	0.011	1.00	--	--	--
Mean Gradient:I(Winter Rain^2)	-0.152±0.053	0.004	1.00	-0.018±0.002	<0.001	1.00	--	--	--
Mean Gradient:Summer Rain	--	--	--	--	--	--	--	--	--
Mean Gradient:I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Prop Lochs:Winter Rain	--	--	--	0.004±0.004	0.345	0.61	--	--	--
PropLochs:I(WinterRain^2)	--	--	--	-0.005±0.004	0.227	0.78	--	--	--
Prop Lochs:Summer Rain	--	--	--	--	--	--	--	--	--
Prop Lochs:I(Summer Rain^2)	--	--	--	--	--	--	--	--	--

A1.7 Time Period 2018 (2014-2018)

A1.7.1 Sea trout catch

River length and Region

A significant interaction between river length and Region highlighted regional differences in sea trout catch in Time Period 2018, indicating that for similar river lengths there were statistically different numbers of sea trout caught in different Regions. This difference in sea trout catch was greater for longer river lengths. The Clyde Coast ($P < 0.001$) and Solway Regions ($P = 0.034$) all had a significantly positive relationship between sea trout catch and river length ($P < 0.001$) (Table A1.12). Three Regions (East, Moray Firth and North East) had a significantly negative relationship between sea trout catch and river length ($P < 0.001$). In some Regions, this relationship was reversed as river length declined. A District with a long river length in the Solway Region reported significantly higher sea trout catches compared to a District with a similar river length in the North East Region. As river length declined, the strength of the effect of the interaction decreased. All other Regions (West Coast, North West, Outer Hebrides and North) showed no significant relationship between sea trout catch and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00 (see Methods for description).

River length and winter rainfall

The interaction between river length and mean winter rainfall was typified by a significant relationship in Time Period 2018 ($P = 0.001$) (Table A1.12). The highest sea trout catches were reported in longer rivers when the mean monthly winter rainfall was below 100mm. Significantly lower sea trout catches were reported in smaller rivers that received the same amount of winter rainfall. As mean rainfall increased, sea trout catch across all rivers declined. In Time Period 2018, there was a smaller difference between sea trout catches caught during periods of high or low winter rainfall across all sized rivers than had been observed in Time Periods 2008 and 2014. Mean winter rainfall values ranged from 55.25mm to 211.57mm in Time Period 2018 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Mean river gradient

The mean river gradient of a District had a significant positive relationship with sea trout catch in Time Period 2018 ($P = 0.016$) (Table A1.12), indicating that as a District's mean gradient increased, so did sea trout catch. Mean river gradient values ranged from 1.97 to

37.92 (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

A1.7.2 Proportional abundance

River length and Region

A significant interaction between river length and Region highlighted regional differences in proportional abundance of sea trout in Time Period 2018, indicating that for similar river lengths there was a statistically different proportional abundance of sea trout caught in different Regions. This difference in proportional abundance was greater in longer river lengths. Three Regions (Clyde Coast (P =0.007), Outer Hebrides (P =0.007) and Solway (P <0.001) (Table A1.12)) had a significant positive relationship between proportional abundance and river length. As river length declined, the strength of the effect of the interaction decreased. The remaining Regions (East, Moray Firth, North, North West and West Coast) showed no significant relationship between proportional abundance and river length. The Importance Value assigned to this interaction by the model dredging process was 1.00.

River length and winter rainfall

In Time Period 2018, there was a significant interaction between river length and mean winter rainfall, which was typified by a significant negative relationship between proportional abundance and winter rainfall (P <0.001) (Table A1.12). For example, a higher proportional abundance of sea trout was observed in long rivers when winter rainfall was low than when rainfall was high. As river length decreased, so did the proportional abundance of sea trout. Smaller rivers saw higher proportions of sea trout when rainfall was low than when rainfall was high. Mean winter rainfall values ranged from 55.25mm to 211.57mm in Time Period 2018 (Table A1.7). The Importance Value assigned to this interaction by the model dredging process was 1.00.

Calcareous geology

The percentage of calcareous geology within a District's catchment area had a significantly negative relationship with proportional abundance in Time Period 2018 (P = 0.004) (Table A1.12) indicating that as the percentage of calcareous geology increased, proportional abundance of sea trout decreased. The percentage of calcareous geology within a District's catchment ranged from 0 to 61.82% The percentage of calcareous geology within a

District's catchment ranged from 0 to 61.82% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Peatland dominance

The percentage of peatland within a District's catchment area was significantly positively correlated with proportional abundance in Time Period 2018 (P=0.012) (Table A1.12), indicating that as peatland dominance increased, proportional abundance increased. Peatland dominance within a District's catchment ranged from 0 to 85.97% (Table A1.1). The Importance Value assigned to this model term by the model dredging process was 1.00.

Combined sewer outflow (CSO's)

In Time Period 2018, the number of CSO's per kilometre was significantly positively correlated with proportional abundance of sea trout (P =0.037) (Table A1.12), indicating that as the number of CSO's per kilometre increased, proportional abundance increased. The Importance Value assigned to this model term by the model dredging process was 1.00.

A1.7.3 Rate of change

Polynomial of sea temperature

The polynomial of mean sea temperature (C°) was found to have a significantly positive correlation with rate of change in Time Period 2018 (P = 0.046) (Table A1.12). For example, the predicted rate of change increases to a value of 0.50 as sea temperatures reach an estimated 11°C, indicating that sea trout populations are increasing at the quickest rate at this temperature. However, once temperatures reach an estimated 11.2°C, the predicted rate of change begins to decline and reaches a value of -0.20 at around 11.7°C, indicating that sea trout populations are declining at a faster rate. Mean sea temperatures ranged from 10.27°C to 12.03°C in Time Period 2008 (Table A1.7). This Time Period reported the second highest mean sea temperatures of the time series at 10.98± 0.03 (mean ± SE). The Importance Value assigned to this model term by the model dredging process was 1.00.

Table A1.12.1 - Time Period 2018 Variable Selection (2014-2018)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P	Importance	Est±SE	P	Importance	Est±SE	P	Importance
Geographic Intercept (Region	5.783±0.452	<0.001	--	0.116±0.023	<0.001	--	0.049±0.125	0.698	--
Coast	-0.279±0.422	0.510	0.470	-0.047±0.022	0.031	only 1 model	-0.035±0.121	0.774	0.290
River Specific Intercept	5.688±0.066	<0.001	--	0.099±0.003	<0.001	--	0.023±0.089	0.798	--
Calcareous	-0.112±0.091	0.217	0.760	-0.011±0.004	0.006	1.000	-0.012±0.045	0.793	0.165
Main River Length	0.569±0.071	<0.001	1.000	0.040±0.004	<0.001	1.000		dropped	
Maximum Altitude	-0.001±0.022	0.951	0.050	-0.001±0.002	0.799	0.110	-0.012±0.046	0.789	0.167
Peat	0.058±0.078	0.458	0.050	0.009±0.004	0.018	1.000		dropped	
Solid Geology	-0.200±0.069	0.004	1.000	-0.006±0.004	0.103	0.920		dropped	
Mean River Gradient	-0.364±0.087	<0.001	1.000	-0.006±0.005	0.268	0.720	-0.008±0.040	0.840	0.143
CSO/km	0.007±0.032	0.836	0.120	0.011±0.004	0.005	1.000	0.013±0.047	0.779	0.173
Flood10	-0.062±0.099	0.529	0.430	-0.001±0.003	0.705	0.250		dropped	
Prop Lochs	0.070±0.111	0.531	0.430	-0.005±0.005	0.336	0.660		dropped	
Climatic Intercept	5.230±0.155	<0.001	--	0.067±0.007	<0.001	--	-0.148±0.128	0.256	--
Sea Temperature	-0.325±0.089	<0.001	1.000	-0.022±0.004	<0.001	1.000		dropped	
I(Sea Temperature^2)	0.299±0.074	<0.001	1.000	0.015±0.004	<0.001	1.000	0.176±0.085	0.043	1.000
Air Temperature		co-correlated			co-correlated			co-correlated	
I(Air Temperature^2)		co-correlated			co-correlated			co-correlated	
Mean Winter Rain	-0.053±0.093	0.568	0.400	-0.014±0.005	0.001	1.000	0.019±0.054	0.731	0.250
I(Mean Winter Rain^2)	0.346±0.089	<0.001	1.000	0.019±0.004	<0.001	1.000	-0.008±0.028	0.769	0.220
Mean Summer Rain	-0.012±0.056	0.832	0.140		dropped		--	--	--
I(Mean Summer Rain^2)		dropped		-0.001±0.002	0.778	0.190	--	--	--
Winter NAO	0.041±0.086	0.638	0.230	0.001±0.002	0.817	0.180	--	--	--

Table A1.12.1 (continued) - Time Period 2018 Variable Selection (2014-2018)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Est±SE	P	Importance	Est±SE	P	Importance	Est±SE	P	Importance
I(Winter NAO^2)	-0.083±0.084	0.323	0.630	-0.001±0.002	0.730	0.230	--	--	--
Summer NAO	co-correlated			co-correlated			co-correlated		
I(Summer NAO^2)	co-correlated			co-correlated			co-correlated		

Table A1.12.2 - Time Period 2018 Averaged Model (2014-2018)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Intercept (Clyde Coast)	4.826±0.172	<0.001	1.000	0.069±0.025	0.007	1.000	--	--	--
Region East	1.334±0.480	0.006	1.000	0.070±0.032	0.032	1.000	--	--	--
Region Moray Firth	0.745±0.307	0.016	1.000	0.016±0.026	0.559	1.000	--	--	--
Region North	1.433±0.344	<0.001	1.000	0.057±0.028	0.040	1.000	--	--	--
Region North East	2.127±0.335	<0.001	1.000	0.108±0.028	<0.001	1.000	--	--	--
Region North West	0.961±0.482	0.048	1.000	0.043±0.026	0.100	1.000	--	--	--
Region Outer Hebrides	2.968±0.540	<0.001	1.000	0.221±0.028	<0.001	1.000	--	--	--
Region Solway	0.991±0.237	<0.001	1.000	0.062±0.018	<0.001	1.000	--	--	--
Region West Coast	-0.120±0.250	0.631	1.000	0.015±0.019	0.432	1.000	--	--	--
Coast	--	--	--	-0.009±0.021	0.657	0.300	--	--	--
Calcareous	--	--	--	-0.009±0.003	0.004	1.000	--	--	--
River Length	1.488±0.185	<0.001	1.000	0.028±0.035	0.428	1.000	--	--	--
Altitude	--	--	--	--	--	--	--	--	--
Peat	--	--	--	0.007±0.003	0.012	1.000	--	--	--
Solid Geology	-0.008±0.031	0.804	0.230	-0.001±0.001	0.744	0.220	--	--	--
CSO/km	--	--	--	0.023±0.011	0.037	1.000	--	--	--

Table A1.12.2 (continued) - Time Period 2018 Averaged Model (2014-2018)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Mean River Gradient	0.170±0.070	0.016	1.000	--	--	--	--	--	--
Flood10	--	--	--	--	--	--	--	--	--
Proportion Lochs	--	--	--	--	--	--	--	--	--
Sea Temperature	0.017±0.068	0.805	0.210		dropped			dropped	
I(Sea Temperature^2)		dropped			dropped		0.173±0.085	0.050	1.000
Air Temperature	--	--	--	--	--	--	--	--	--
I(Air Temperature^2)	--	--	--	--	--	--	--	--	--
Winter Rain	-0.007±0.075	0.923	1.000	-0.008±0.003	0.016	1.000	--	--	--
I(Winter Rain^2)		dropped			dropped		--	--	--
Summer Rain	--	--	--	--	--	--	--	--	--
I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Winter NAO	--	--	--	--	--	--	--	--	--
I(Winter NAO^2)	--	--	--	--	--	--	--	--	--
Summer NAO	--	--	--	--	--	--	--	--	--
I(Summer NAO^2)	--	--	--	--	--	--	--	--	--
Population Variance	--	--	--	--	--	--	-0.029±0.065	0.659	0.340
Region East: Main River	-1.634±0.271	<0.001	1.000	-0.037±0.036	0.306	1.000	--	--	--
Region Moray Firth: River Length	-1.283±0.269	<0.001	1.000	-0.001±0.038	0.971	1.000	--	--	--
Region North: River Length	-0.347±0.656	0.599	1.000	0.025±0.054	0.644	1.000	--	--	--
Region North East: River Length	-2.111±0.378	<0.001	1.000	-0.096±0.030	0.002	1.000	--	--	--
Region North West: River Length	1.085±0.848	0.202	1.000	0.054±0.050	0.279	1.000	--	--	--
Region Outer Hebrides:River Length	-0.154±0.883	0.861	1.000	0.140±0.052	0.007	1.000	--	--	--

Table A1.12 (continued) - Time Period 2018 Averaged Model (2014-2018)									
	Sea Trout Catch			Proportion Abundance			Rate of Change		
Variable	Estimate±SE	P	Importance	Estimate±SE	P	Importance	Estimate±SE	P	Importance
Region Solway: Main River	1.205±0.584	0.040	1.000	0.151±0.043	<0.001	1.000	--	--	--
Region West Coast: River Length	-0.580±0.342	0.091	1.000	-0.001±0.037	0.993	1.000	--	--	--
River Length: Winter Rain	-0.270±0.079	0.001	1.000	-0.019±0.003	<0.001	1.000	--	--	--
River Length: I(Winter Rain^2)	--	--	--		dropped		--	--	--
River Length:Summer Rain	--	--	--	--	--	--	--	--	--
River Length: I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Mean Gradient:Winter Rain		dropped		--	--	--	--	--	--
Mean Gradient:I(Winter Rain^2)		dropped		--	--	--	--	--	--
Mean Gradient:Summer Rain	--	--	--	--	--	--	--	--	--
Mean Gradient:I(Summer Rain^2)	--	--	--	--	--	--	--	--	--
Prop Lochs:Winter Rain	--	--	--	--	--	--	--	--	--
PropLochs:I(WinterRain^2)	--	--	--	--	--	--	--	--	--
Prop Lochs:Summer Rain	--	--	--	--	--	--	--	--	--
Prop Lochs:I(Summer Rain^2)	--	--	--	--	--	--	--	--	--

Appendix 2: Supplementary Information for Chapter 3

(Influences of open net-pen aquaculture on anadromous sea trout (*Salmo trutta*) populations on the west coast of Scotland over the last 20 years)

The following supplementary information was compiled to provide further information about the selected variables used in Chapter 3, as well as the model outputs of the model dredging process.

Table A2.1. List of variables used in modelling in this study, including potential drivers of change in sea trout populations used as model explanatory variables, their definitions, justification for inclusion, and examples of their importance as well as the source of the data used. (* - the 2nd order polynomial term of a variable that was included in the modelling process; [a] - Marine Scotland Science, 2019; [Ω] - Scottish Environment Protection Agency, 2019; [λ] - Met Office, 2019; [Φ] - Climate Research Unit, 2019; [b] – Scottish Government, 2019.

Genre	Variable	Minimum Range	Maximum Range	Type/data per category	Reasoning	Source	Example(s)
Measures of abundance	Sea trout catch	0.00	2978.00	Annual reported district sea trout abundance (17 years of data/District)		MSS [a]	
	Rate of change	-0.22	0.17	Change in district sea trout abundance over time; calculated for each District		Calculated by author	
	Proportionate abundance	<0.001	27.18	Percentage of district annual sea trout abundance contributing to national annual total		Calculated by author	
	Population variance	27.62	766.61	Standard deviation of District sea trout abundance; calculated for each District		Calculated by author	
	Biomass rate of change	-0.03	0.28	Change in farm biomass production over time; calculated for each district		Calculated by author	
Geographic	District	0.00	47.00	Geographic locations associated with a river or group of rivers designated by MSS	Changes in abundance between geographic location	MSS [a]	Youngson *et al.*, 2002

Table A2.1 (continued). List of variables used in modelling in this study, including potential drivers of change in sea trout populations used as model explanatory variables, their definitions, justification for inclusion, and examples of their importance as well as the source of the data used. (* - the 2nd order polynomial term of a variable that was included in the modelling process; [a] - Marine Scotland Science, 2019; [Ω] - Scottish Environment Protection Agency, 2019; [λ] - Met Office, 2019; [Φ] - Climate Research Unit, 2019; [b] – Scottish Government, 2019.

Genre	Variable	Minimum Range	Maximum Range	Type/data per category	Reasoning	Source	Example(s)
River specific variables	% Calcareous geology	0.00	61.82	% of calcareous geology within a catchment (1:250K scale)	River characteristics that have been shown to influence *S. trutta* populations	SEPA[Ω]	Solomon &Templeton, 1976
	River length	3.40	1403.58	the sum of all freshwater catchment river lengths in a District (km)		SEPA[Ω]	Bohlin *et al*., 2001; Armstrong *et al*., 2003
	Maximum altitude	265.00	1346.00	the highest point of altitude in a District		SEPA[Ω]	Bohlin *et al*., 2001
	Peatland dominance	0.00	85.97	% of peat geology within a District's catchment(1:625 scale)		SEPA[Ω]	Marttila *et al*., 2018
	% Solid geology	9.50	87.69	% of solid geology at surface within a District's catchment, remaining % is drift geology		SEPA[Ω]	Armstrong *et al*., 2003
	Mean river gradient	1.97	37.92	mean gradient of catchment in a District		SEPA[Ω]	Bohlin *et al*., 2001
	Combined sewer outflow (CSO)/km	0.00	0.35	the number of combined sewer overflows (CSO) per km in District		SEPA[Ω]	Armstrong *et al*., 2003
	Flooding Likelihood (10 year)	0.53	8.18	the % of the District's catchment within a 1:10 year predictive flood area, derived from flood risk maps		SEPA[Ω]	Fausch 2007; May *et al*. 2018
	Proportion Lochs	0.00	43.49	% of loch surface area within a District's catchment	Important habitat for Scottish *S. trutta*	SEPA[Ω], calculated by author	Campbell 1971

Table A2.1 (continued). List of variables used in modelling in this study, including potential drivers of change in sea trout populations used as model explanatory variables, their definitions, justification for inclusion, and examples of their importance as well as the source of the data used. (* - the 2nd order polynomial term of a variable that was included in the modelling process; [a] - Marine Scotland Science, 2019; [Ω] - Scottish Environment Protection Agency, 2019; [λ] - Met Office, 2019; [Φ] - Climate Research Unit, 2019; [b] – Scottish Government, 2019.

Genre	Variable	Minimum Range	Maximum Range	Type/data per category	Reasoning	Source	Example(s)
Climatic	Mean sea temperature	10.31	12.13	Annual mean sea temperature (°C); assigned by District location	Increasing temperatures can affect survival	Hughes et al., 2018	Honkanen *et al.*, 2018
	I(Mean sea temperature^2)*	-	-	2nd order polynomial term of sea temperature (°C)	Negative effects from extreme temperatures	Author	Elliot & Elliot 2010
	Mean air temperature	6.20	9.05	Annual mean air temperature (°C); assigned by District location	Increasing temperatures can affect survival	Met Office[λ]	Isaak *et al.*, 2012
	I(Mean air temperature^2)*	-	-	2nd order polynomial term of air temperature (°C)	Negative effects from extreme temperatures	Author	Isaak *et al.*, 2012
	Mean winter rain	112.80	221.22	Mean rain per month (mm) calculated from October Year X to March Year Y	Affecting flow/discharge and temperature	Met Office[λ]	Honkanen *et al.*, 2018
	I(Mean winter rain^2)*	-	-	2nd order polynomial term of mean winter rain (mm)	Effects from extremes, floods or droughts	Author	Warren *et al.*, 2015
	Winter rain variance	25.81	30.35	Standard deviation of mean winter rain (only used in rate of change models)	Erratic changes effect long term population trends	Author	

Table A2.1 (continued). List of variables used in modelling in this study, including potential drivers of change in sea trout populations used as model explanatory variables, their definitions, justification for inclusion, and examples of their importance as well as the source of the data used. (* - the 2nd order polynomial term of a variable that was included in the modelling process; [a] - Marine Scotland Science, 2019; [Ω] - Scottish Environment Protection Agency, 2019; [λ] - Met Office, 2019; [Φ] - Climate Research Unit, 2019; [b] – Scottish Government, 2019.

Genre	Variable	Minimum Range	Maximum Range	Type/data per category	Reasoning	Source	Example(s)
Climatic	Mean summer rain	75.10	137.87	Mean rain per month (mm) calculated from April Year Y to September Year Y	Affecting flow/discharge and temperature	Met Office[λ]	Honkanen *et al.*, 2018
	I(Mean summer rain^2)*	-	-	2nd order polynomial term of mean summer rain (mm)	Effects from extremes, floods or droughts	Author	Warren *et al.*, 2015
	Summer rain variance	13.36	15.88	Standard deviation of mean summer rain (only used in rate of change models)	Erratic changes effect long term population trends	Author	
	Winter NAO	-1.78	1.72	Mean NAO per month calculated from October Year X to March Year Y	Influence on major weather events	Climate Research Unit[Φ]	Honkanen *et al.*, 2018
	I(Winter NAO^2)*	-	-	2nd order polynomial term of winter NAO	Effects from extreme weather	Author	Sarafanov 2009
	Summer NAO	-1.78	1.45	Mean NAO per month calculated from April Year Y to September Year Y	Influence on major weather events	Climate Research Unit[Φ]	Honkanen *et al.*, 2018
	I(Summer NAO^2)*	-	-	2nd order polynomial term of summer NAO	Effects from extreme weather	Author	Sarafanov 2009

Table A2.1 (continued). List of variables used in modelling in this study, including potential drivers of change in sea trout populations used as model explanatory variables, their definitions, justification for inclusion, and examples of their importance as well as the source of the data used. (* - the 2nd order polynomial term of a variable that was included in the modelling process; [a] - Marine Scotland Science, 2019; [Ω] - Scottish Environment Protection Agency, 2019; [λ] - Met Office, 2019; [Φ] - Climate Research Unit, 2019; [b] – Scottish Government, 2019.

Genre	Variable	Minimum Range	Maximum Range	Type/data per category	Reasoning	Source	Example(s)
Aquaculture	Biomass (30km)	0.00	15088.00	Sum of aquaculture biomass (T) produced within 30km of a District; 30 km measured from river mouth to farm location by sea distance	Evidence demonstrating aquaculture production influences on salmonid survival at sea	Scottish Gov. [b]	Pentson & Davies, 2008; Moore *et al*., 2018

Table A2.2. Net-pen presence/absence variable selection model outputs for three measures of abundance. The "Importance" column reports the Importance value assigned to each variable from the dredge process. "Co-correlated" variables were found to be co-correlated with at least one more ecologically relevant variable during data exploration and thus dropped from variable selection process. "Dropped" variables indicates that the variable was dropped by the dredge process as it was not important to the model. "1 model" indicates that the dredge process produced a single model because all variables were important in predicting the measure of abundance.

	Sea Trout Catch			Proportionate Abundance			Rate of Change		
Variable	Est±SE	P	Importance	Est±SE	P	Importance	Est±SE	P	Importance
River Specific Intercept	5.232±0.039	<0.001	--	0.116±0.003	<0.001	--	0.001±0.014	0.99	--
% Calcareous Geology	-0.532±0.047	<0.001	1 model	-0.026±0.003	<0.001	1 model	0.006±0.046	0.887	0.070
Main River Length	0.585±0.049	<0.001	1 model	0.045±0.003	<0.001	1 model	0.015±0.065	0.814	0.100
Maximum Altitude	-0.385±0.061	<0.001	1 model	-0.027±0.004	<0.001	1 model	dropped		
Peatland Dominance	0.143±0.049	0.004	1 model	0.013±0.003	<0.001	1 model	0.014±0.063	0.822	0.100
% Solid Geology	-0.505±0.055	<0.001	1 model	-0.017±0.004	<0.001	1 model	-0.081±0.143	0.577	0.340
Mean River Gradient	0.210±0.062	0.001	1 model	0.014±0.004	0.001	1 model	dropped		
CSO/km	co-correlated			co-correlated			co-correlated		
Flood10	0.321±0.044	<0.001	1 model	0.008±0.003	0.004	1 model	-0.172±0.168	0.313	0.690
Prop Lochs	co-correlated			co-correlated			co-correlated		
Climatic Intercept	5.166±0.095	<0.001	--	0.089±0.005	<0.001	--	-0.047±0.182	0.799	--
Sea Temperature	-0.129±0.050	0.01	1.000	-0.016±0.003	<0.001	1.000	-0.124±0.203	0.544	0.370
I(Sea Temperature^2)	0.315±0.040	<0.001	1.000	0.021±0.003	<0.001	1.000	0.048±0.114	0.675	0.290
Air Temperature	co-correlated			co-correlated			co-correlated		
I(Air Temperature^2)	co-correlated			co-correlated			co-correlated		
Mean Winter Rain	0.074±0.063	0.238	0.740	0.001±0.001	0.931	0.090	-0.193±0.231	0.408	0.580
I(Mean Winter Rain^2)	0.036±0.049	0.466	0.500	0.005±0.003	0.111	0.900	co-correlated		
Mean Summer Rain	0.036±0.048	0.464	0.520	0.006±0.003	0.038	1.000	co-correlated		
I(Mean Summer Rain^2)	dropped			0.001±0.001	0.791	0.220	co-correlated		
Winter NAO	co-correlated			co-correlated			--		

Table A2.2 (continued). Net-pen presence/absence variable selection model outputs for three measures of abundance. The “Importance” column reports the Importance value assigned to each variable from the dredge process. “Co-correlated” variables were found to be co-correlated with at least one more ecologically relevant variable during data exploration and thus dropped from variable selection process. “Dropped” variables indicates that the variable was dropped by the dredge process as it was not important to the model. “1 model” indicates that the dredge process produced a single model because all variables were important in predicting the measure of abundance.

Variable	Sea Trout Catch			Proportionate Abundance			Rate of Change		
	Est±SE	P	Importance	Est±SE	P	Importance	Est±SE	P	Importance
I(Winter NAO^2)	co-correlated			co-correlated			--		
Summer NAO	-0.002±0.014	0.882	0.070	-0.002±0.003	0.443	0.550	--		
I(Summer NAO^2)	-0.049±0.048	0.307	0.680	-0.001±0.001	0.951	0.090	--		

Table A2.3. Net-pen presence/absence averaged model outputs for three measures of abundance. The “Importance” column reports the Importance value assigned to each variable from the dredge process. “Co-correlated” variables were found to be co-correlated with at least one more ecologically relevant variable during data exploration and thus dropped from variable selection process. “Dropped” variables indicates that the variable was dropped by the dredge process as it was not important to the model. “1 model” indicates that the dredge process produced a single model because all variables were important in predicting the measure of abundance.

	Sea Trout Catch			Proportionate Abundance			Rate of Change		
Variable	Est±SE	P	Importance	Est±SE	P	Importance	Est±SE	P	Importance
Intercept	4.202±0.129	<0.001	--	0.063±0.008	<0.001	--	0.064±0.214	0.770	--
% Calcareous Geology	-0.501±0.046	<0.001	1 model	-0.028±0.003	<0.001	1.000		--	
Main River Length	1.143±0.056	<0.001	1 model	0.069±0.003	<0.001	1.000		--	
Maximum Altitude	-0.252±0.059	<0.001	1 model	-0.020±0.003	<0.001	1.000		--	
Peatland Dominance	0.175±0.047	<0.001	1 model	0.014±0.003	<0.001	1.000		--	
Mean River Gradient	0.192±0.064	0.003	1 model	0.009±0.004	0.022	1.000		--	
% Solid Geology	-0.638±0.059	<0.001	1 model	-0.030±0.004	<0.001	1.000		--	
Flood10	0.377±0.0464	<0.001	1 model	0.018±0.003	<0.001	1.000		--	
Sea Temperature	0.125±0.069	0.07	1 model	0.002±0.004	0.565	1.000		--	
I(Sea Temperature^2)	-0.087±0.057	0.124	1 model	-0.004±0.003	0.248	1.000		--	
Winter Rain		--		-0.007±0.005	0.156	0.870		--	
I(Winter Rain^2)		--		0.001±0.001	0.745	0.200		--	
Summer Rain		--		0.003±0.003	0.215	1.000		--	
Population Variance		--			--		0.024±0.082	0.775	0.216
Farm Presence	0.758±0.163	<0.001	1 model	0.043±0.010	<0.001	1.000	-0.091±0.223	0.688	0.278
Mean Gradient:Winter Rain		--		-0.005±0.003	0.105	0.870		--	
Farm P/A: Sea Temperature	-0.339±0.091	<0.001	1 model	-0.022±0.006	<0.001	1.000		--	
Farm P/A: I(Sea Temperature^2)	0.407±0.076	<0.001	1 model	0.027±0.005	<0.001	1.000		--	
Farm P/A: Winter Rain		--		0.012±0.007	0.099	0.870		--	
Farm P/A: Summer Rain		--		0.001±0.002	0.832	0.150		--	

Table A2.3 (continued). Net-pen presence/absence averaged model outputs for three measures of abundance. The “Importance” column reports the Importance value assigned to each variable from the dredge process. “Co-correlated” variables were found to be co-correlated with at least one more ecologically relevant variable during data exploration and thus dropped from variable selection process. “Dropped” variables indicates that the variable was dropped by the dredge process as it was not important to the model. “1 model” indicates that the dredge process produced a single model because all variables were important in predicting the measure of abundance.

Variable	Sea Trout Catch			Proportionate Abundance			Rate of Change		
	Est±SE	P	Importance	Est±SE	P	Importance	Est±SE	P	Importance
Farm P/A: River Length	-0.857±0.092	<0.001	1 model	-0.048±0.006	<0.001	1.000	--		
River Length:Summer Rain	--			-0.006±0.002	0.003	1.000	--		
River Length:Winter Rain	--			-0.001±0.002	0.827	0.150	--		

Table A2.4. Net-pen biomass variable selection model outputs for three measures of abundance. The “Importance” column reports the Importance value assigned to each variable from the dredge process. “Co-correlated” variables were found to be co-correlated with at least one more ecologically relevant variable during data exploration and thus dropped from variable selection process. “Dropped” variables indicates that the variable was dropped by the dredge process as it was not important to the model. “1 model” indicates that the dredge process produced a single model because all variables were important in predicting the measure of abundance.

Variable	Sea Trout Catch			Proportionate Abundance			Rate of Change		
	Est±SE	P	Importance	Est±SE	P	Importance	Est±SE	P	Importance
River Specific Intercept	2.626±0.696	<0.001	--	0.108±0.026	<0.001	--	0.001±0.170	0.99	--
% Calcareous Geology	-0.592±0.060	<0.001	1.000	-0.039±0.003	<0.001	1.000	dropped		
Main River Length	0.358±0.089	<0.001	1.000	0.016±0.005	0.002	1.000	dropped		
Maximum Altitude	-0.302±0.064	<0.001	1.000	-0.016±0.004	<0.001	1.000	dropped		
Peatland Dominance	0.313±0.072	<0.001	1.000	0.021±0.004	<0.001	1.000	dropped		
% Solid Geology	-0.777±0.056	<0.001	1.000	-0.043±0.003	<0.001	1.000	dropped		
Mean River Gradient	0.018±0.048	0.706	0.320	-0.001±0.002	0.687	0.280	dropped		
CSO/km	-11.619±3.225	<0.001	1.000	-0.044±0.121	0.713	0.260	dropped		
Flood10	0.476±0.052	<0.001	1.000	0.023±0.003	<0.001	1.000	-0.021±0.206	0.322	0.640
Prop Lochs	co-correlated			co-correlated			co-correlated		
Climatic Intercept	5.153±0.123	<0.001		0.089±0.005	<0.001	--	0.001±0.16	0.99	--
Sea Temperature	-0.492±0.072	<0.001	1.000	-0.043±0.004	<0.001	1.000	-0.066±0.155	0.674	0.240
I(Sea Temperature^2)	0.316±0.052	<0.001	1.000	0.028±0.003	<0.001	1.000	dropped		
Air Temperature	co-correlated			co-correlated			co-correlated		
I(Air Temperature^2)	co-correlated			co-correlated			co-correlated		
Mean Winter Rain	0.159±0.058	0.007	1.000	0.003±0.004	0.349	0.640	-0.166±0.210	0.438	0.560
I(Mean Winter Rain^2)	-0.017±0.040	0.667	1.000	0.001±0.002	0.782	0.200	co-correlated		

Table A2.4 (continued). Net-pen biomass variable selection model outputs for three measures of abundance. The "Importance" column reports the Importance value assigned to each variable from the dredge process. "Co-correlated" variables were found to be co-correlated with at least one more ecologically relevant variable during data exploration and thus dropped from variable selection process. "Dropped" variables indicates that the variable was dropped by the dredge process as it was not important to the model. "1 model" indicates that the dredge process produced a single model because all variables were important in predicting the measure of abundance.

Variable	Sea Trout Catch			Proportionate Abundance			Rate of Change		
	Est±SE	P	Importance	Est±SE	P	Importance	Est±SE	P	Importance
Mean Summer Rain	0.132±0.055	0.017	1.000	0.004±0.004	0.319	0.690	co-correlated		
I(Mean Summer Rain^2)	-0.064±0.056	0.258	1.000	-0.001±0.001	0.848	0.110	co-correlated		
Winter NAO	co-correlated			co-correlated			--		
I(Winter NAO^2)	co-correlated			co-correlated			--		
Summer NAO	-0.146±0.053	0.006	1.000	-0.011±0.003	0.001	1.000	--		
I(Summer NAO^2)	-0.159±0.052	0.003	1.000	-0.009±0.003	0.003	1.000	--		

Table A2.5. Net-pen biomass averaged model outputs for three measures of abundance. The “Importance” column reports the Importance value assigned to each variable from the dredge process. “Co-correlated” variables were found to be co-correlated with at least one more ecologically relevant variable during data exploration and thus dropped from variable selection process. “Dropped” variables indicates that the variable was dropped by the dredge process as it was not important to the model. “1 model” indicates that the dredge process produced a single model because all variables were important in predicting the measure of abundance.

Variable	Sea Trout Catch			Proportionate Abundance			Rate of Change		
	Est±SE	P	Importance	Est±SE	P	Importance	Est±SE	P	Importance
Intercept	15.873±19.037	0.405	--	0.486±1.207	0.687	--	-0.001±0.174	0.99	--
% Calcareous Geology	-0.370±0.058	<0.001	1.000	-0.027±0.003	<0.001	1 model	--		
River Length	0.361±0.116	0.002	1.000	0.024±0.007	<0.001	1 model	--		
Maximum Altitude	-0.147±0.061	0.016	1.000	-0.007±0.003	0.03	1 model	--		
Peatland Dominance	0.216±0.053	<0.001	1.000	0.025±0.003	<0.001	1 model	--		
Mean River Gradient	--			--			--		
% Solid Geology	-0.659±0.058	<0.001	1.000	-0.034±0.003	<0.001	1 model	--		
CSO/km	0.103±0.899	0.909	0.060	--			--		
Flood10	0.358±0.049	<0.001	1.000	0.015±0.003	<0.001	1 model	--		
Sea Temperature	-0.163±0.062	0.008	1.000	-0.023±0.002	<0.001	1 model	--		
I(Sea Temperature^2)	0.287±0.051	<0.001	1.000	0.022±0.003	<0.001	1 model	--		
Winter Rain	0.063±0.047	0.185	1.000	--			--		
I(Winter Rain^2)	dropped			--			--		
Summer Rain	0.111±0.048	0.022	1.000	--			--		
Summer NAO	-0.069±0.053	0.192	0.800	-0.008±0.003	0.004	1 model	--		
I(Summer NAO^2)	-0.018±0.035	0.616	0.300	-0.007±0.002	0.005	1 model	--		
Year	-0.005±0.009	0.566	0.370	-0.001±0.001	0.754	1 model	--		
Biomass ROC	--			--			0.055±0.129	0.675	0.257

Table A2.5 (continued). Net-pen biomass averaged model outputs for three measures of abundance. The "Importance" column reports the Importance value assigned to each variable from the dredge process. "Co-correlated" variables were found to be co-correlated with at least one more ecologically relevant variable during data exploration and thus dropped from variable selection process. "Dropped" variables indicates that the variable was dropped by the dredge process as it was not important to the model. "1 model" indicates that the dredge process produced a single model because all variables were important in predicting the measure of abundance.

	Sea Trout Catch			Proportionate Abundance			Rate of Change		
Variable	Est±SE	P	Importance	Est±SE	P	Importance	Est±SE	P	Importance
Population Variance	--			--			0.024±0.091	0.793	0.168
Farm Biomass	-0.283±0.069	<0.001	1.000	-0.017±0.004	<0.001	1 model	0.028±0.096	0.777	0.178
Farm Biomass: Sea Temp	-0.029±0.055	0.599	0.330	-0.010±0.003	0.005	1 model	--		
Farm Biomass: I(Sea Temp^2)	0.143±0.049	0.004	1.000	0.013±0.003	<0.001	1 model	--		
Farm Biomass: River Length	-0.043±0.087	0.616	0.330	-0.013±0.006	0.024	1 model	--		
Farm Biomass: Winter Rain	0.119±0.042	0.005	1.000	--			--		
Farm Biomass: Summer Rain	0.029±0.045	0.509	0.440	--			--		

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